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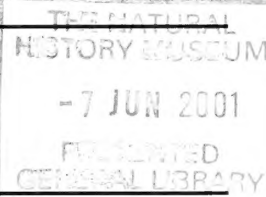
Fossil pseudasturid birds (Aves, Pseudasturidae) from the London Clay

GARETH J. DYKE

Department of Ornithology, American Museum of Natural History, Central Park W at 79ᵗʰ Street, New York NY 10024, USA.

SYNOPSIS. Fossil remains from the Lower Eocene (Ypresian) London Clay Formation of England are referred to the extinct higher-order group of birds, the Pseudasturidae Mayr. This material includes the specimen BMNH A 5193, referred by Harrison (1982) to the taxon '*Primobucco' olsoni* Feduccia & Martin, previously the oldest published record of a piciform bird (barbets and relatives) known from the fossil record. The description of three-dimensionally preserved tarsometatarsi from the London Clay confirms the fully zygodactyl nature of the pseudasturid foot (fourth toe directed backwards).

INTRODUCTION

The extinct avian family Pseudasturidae was erected by Mayr (1998) for the reception of a number of small, zygodactyl, landbirds that are known from the Lower-Middle Eocene of Europe and North America. Mayr (1998) diagnosed this higher-taxon on the basis of a number of putatively derived (apomorphic) characters of the skull, vertebrae and limbs and included within the group two species from the Middle Eocene deposit of Grube Messel, Hessen, Germany (*Pseudastur macrocephalus* [Fig. 1] and an unnamed taxon), as well as the enigmatic taxon '*Primobucco' olsoni* (Feduccia & Martin, 1976) known from the Eocene of North America, and from the London Clay (see Mayr, 1998).

In this paper, I present the descriptions of a number of fossil specimens from the London Clay Formation of England that are referable to the Pseudasturidae, as defined by Mayr (1998). Amongst this material is a proximal portion of tarsometatarsus (BMNH A 5193) that was classified by Harrison (1982) within the order Piciformes (barbets and relatives), previously the oldest published record for this group of modern birds. The three-dimensional preservation of the London Clay specimens serves to confirm the supposition of Mayr (1998) that the pseudasturid birds had a fully developed zygodactyl foot (fourth toe turned backwards to facilitate perching and climbing) with a prominent sehnenhalter or medial or plantar projection of the fourth trochlea (Steinbacher, 1935).

The fossil specimens discussed here are housed in the collections of The Natural History Museum, London, UK, (Palaeontology Department; BMNH A), the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF), the Wyoming Dinosaur Center, Thermopolis, USA (collection POHL, examined in Frankfurt), and the Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK). Recent osteological specimens examined during the course of this work are held in the ornithological collections of The Natural History Museum, Tring, Hertfordshire, UK (BMNH S). Anatomical nomenclature used follows Howard (1929) and Baumel & Witmer (1993).

SYSTEMATIC PALEONTOLOGY

Class **AVES** Linnaeus, 1758
Order **INCERTAE SEDIS**
Family **PSEUDASTURIDAE** Mayr, 1998
Genus and Species *INDET*.

Referred London Clay specimens

MATERIAL. BMNH A 6218 (Fig 2A), associated bones consisting of: a partially complete right scapula (lacking extreme lateral portion of extremitas caudalis); a partially complete right coracoid (lacking the processus procoracoideus, lateral extremity of processus acrocoracoideus and lateral portion of facies articularis sternalis); a proximal end of a left coracoid and portion of shaft; a proximal end of a right humerus and portion of shaft; a nearly complete left femur (lacking portions of condylus medialis, sulcus intercondylaris, condylus lateralis and crista trochanteris). BMNH A 6184 (Fig. 2F), a distal end of a left tarsometatarsus and portion of shaft.

GEOLOGICAL AGE AND LOCALITIES. BMNH A 6218 was collected from an unknown horizon within the London Clay Formation at Walton-on-the-Naze, Essex, England by Mr. W. George in 1977 (his original collectors number is unknown). BMNH A 6184 was collected from within division D–E of the London Clay Formation at Warden Point, Isle of Sheppey, Kent, England by Alleyn School (donated via Mr. Salmon) in 1983. The age of the Walton and Warden beds of the London Clay Formation (Bed A2; King, 1981) are approximately 54.4 Mya (after Harland *et al.*, 1990; Berggren *et al.*, 1995).

BMNH A 6218

SCAPULA (Fig. 2B). The blade of the scapula is broad and gently curved although the extremitas caudalis is lacking. The facies articularis humeralis is flat and ovate in form and is not excavated. The tuberculum coracoideum is small and obsolete, the acromion is rounded and blunt.

CORACOID (Fig. 2A). The processus acrocoracoideus is very abrupt and blunt with almost no point. The brachial tuberosity is very markedly folded over towards the processus procoracoideus; this tuberosity only extends laterally to level with the edge of the cotyla scapularis. The margin between the glenoid and scapular facets is raised and pronounced, the scapular facet is shallow but has a raised distal margin (much higher than the shaft). On both of the preserved coracoids, the extremity of the procoracoid process is broken but this does appear to have been flat laterally. There is a small foramen nervi supracoracoidei in the middle of the shaft distal to the sternal facet.

Overall, the coracoid shaft is straight, but there is a slight kink immediately distal to the foramen nervi supracoracoidei. The sterno-coracoid impression is rectangular and shallowly excavated centrally; the distal borders of this impression are raised and the angulus
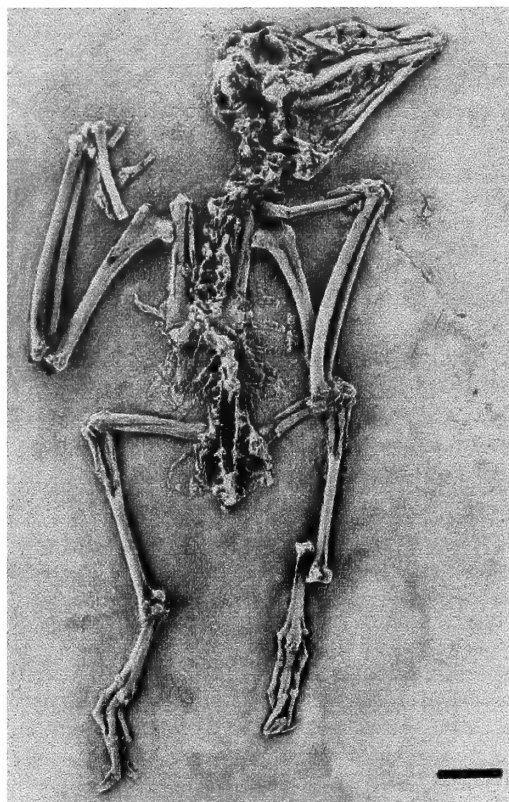
Fig. 1 *Pseudastur macrocephalus* holotype specimen (WDC-C-MG-94), covered with ammonium chloride to enhance contrast. Scale bar = 10mm. This figure reproduced from Mayr (1998) with permission, Forschunsinstitut Senckenberg.

Fig. 2 Pseudasturid specimens from the London Clay Formation. **A–E,** BMNH A 6218; **A,** portion of left coracoid; **B,** left scapula; **C,** left femur; **D,** portion of right humerus; **E,** right coracoid. **F,** BMNH A 6184, distal end of a left tarsometatarsus. **G,** BMNH A 6224, proximal right tarsometatarsus. All figures are × 2.

medialis is pointed. The sternal facet is shallow, rectangular and located on the plane of the coracoid surface (not obliquely under the proximal end).

HUMERUS (Fig. 2D). In caudal view, the tuberculum dorsale (although broken distally) appears to point distally. The incisura capitis and tuberculum ventrale are obscured by sediment, although the latter appears to have been well developed. The fossa pneumotricipitalis is shallow, shelf-like and bordered laterally by a pronounced attachment for the musculus infraspinatus that is well developed and square-shaped. The lateral margin of the crista deltopectoralis is extremely curved (almost semi-circular) in outline, the crista bicipitalis meets the shaft at about 70 degrees; the crus dorsale fossae is obscured.

FEMUR (Fig. 2C). This is a very short and stocky element (relative to the preserved humeral length; see measurements). The fossa trochanteris is shallow and obsolete; the trochanter is not well developed and is rounded and blunt. The iliac facet is flat and in line with the head of the femur. The femoral head is turned distally and overhangs the shaft somewhat; the angle between the head and the shaft is about 90 degrees. The shaft is stocky and straight with little lateral curvature, there is no offset between the proximal and distal ends.

BMNH A 6184

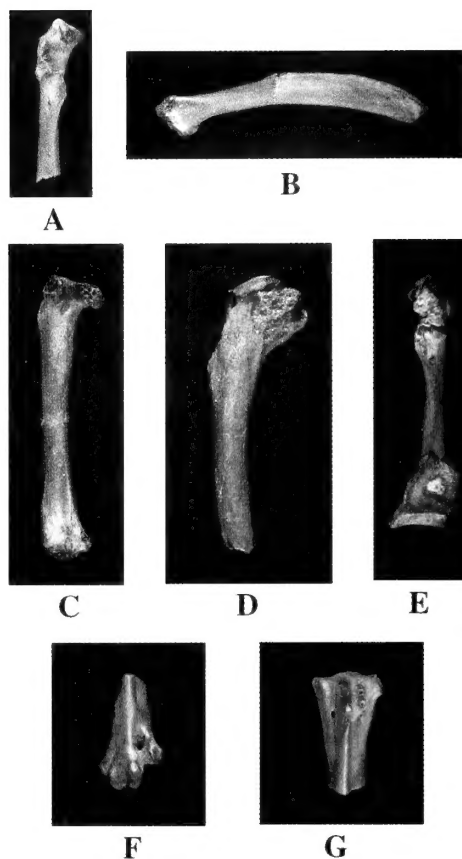TARSOMETATARSUS (Fig. 2F). A large foramen vasuculare distale

is present that is ovate in outline. In plantar view, the surface of the tarsometatarsus is smoothly excavated distally. The trochlea metatarsi IV is broad anteriorly and bears a sehnenhalter (Steinbacher, 1935) that is not separated from the remainder of the trochlea by a groove (contrary to all known psittaciforms; Mayr & Daniels, 1998). On the lateral surface of the retroverted portion of trochlea metatarsi IV there is a marked and rounded prominence. The trochlea metatarsi III is broad and has a marked medial furrow that is bordered by two very prominent lateral ridges. This trochlea is separated from trochlea metatarsi II by a U-shaped depression. Trochlea metatarsi II is square is shape and very flat across the surface of the distal end (i.e. knuckle-view).

Measurements

BMNH A 6218: humerus, total preserved length – 15mm, width of caput humeri – 2mm (insicura capitis infilled with sediment); right coracoid, total length – 14mm; length acrocoracoid to procoracoid – 1.2mm; proximal portion left coracoid, total preserved length – 8mm; length acrocoracoid to procoracoid – 1.3mm; left femur, total length – 16mm; right scapula, total length – 15mm.

BMNH A 6184: tarsometatarsus, total preserved length – 5.2mm

Tentatively referred London Clay specimens

MATERIAL. BMNH A 6224 (Fig. 2G), a proximal end of a right tarsometatarsus and portion of shaft (lacking the crista intermediae hypotarsi). BMNH A 5193 (Fig. 3), a proximal end of a right tarsometatarsus (referred to '*Primobucco*' *olsoni* Feduccia & Martin [Aves, Piciformes] by Harrison, 1982). A complete description of this element was provided by Harrison (1982).

GEOLOGICAL AGE AND LOCALITIES. Both the specimens BMNH A 6224 and A 5193 were collected from divisions D–E of the London Clay Formation at Warden Point, Isle of Sheppey, Kent, England (A 6224 collected and presented by Mr. D. Ward in 1982; A 5193 collected and presented by Mr. S. Silverstein in 1980). The age of these beds of the London Clay Formation is approximately 54.4 Mya (after Harland *et al.*, 1990; Berggren *et al.*, 1995).

BMNH A 6224

TARSOMETATARSUS (Fig. 2G). The proximal tarsometatarsus of BMNH A 6224 has a smoothly flattened medial shaft and a flat hypotarsus; the rims of the medial and lateral cotyles (cotylae mediale and laterale) extend distally to about the same level, the area intercotylaris is not raised significantly above the surface of the cotyles. On the proximal surface, both the cotyles are rounded in outline and have raised lateral rims. There are two preserved cristae intermediae hypotarsi. Two oblong proximal foramina are seen on the surface of the shaft; the outer one is somewhat larger but they are both at the same level on the proximal shaft.

Measurements

BMNH A 6224: proximal right tarsometatarsus, total preserved length – 5.2mm, medio-lateral width of hypotarsus – 2.2mm.

BMNH A 5193: proximal right tarsometatarsus, total preserved length – 7.8mm, width of distal end – 2.1mm, width at tibialis anticus scar – 1.3mm (Harrison, 1982).

COMPARISONS AND REMARKS

Although the tarsometatarsi are clearly visible in dorsal view on the Messel pseudasturid specimens, detailed comparisons of this element are only possible between BMNH A 6184 and the well preserved tarsometatarsi of *Pseudastur macrocephalus* (WDC-C-MG-94; Mayr, 1998: text-fig. 1). *P. macrocephalus* and BMNH A 6184 are an almost exact match in terms of size and shape; in both specimens, trochlea metatarsi III is very broad (compared to the trochlea for metatarsals II and IV) and is extended far distally (especially with respect to trochlea metatarsi IV, which is small and located proximally on the shaft). Again, in both specimens there is a prominent medial furrow on the distal trochlea metatarsi III and trochlea metatarsi IV is turned somewhat plantarly to form a small phlange. Based on the characters outlined by Mayr (1998), the specimen BMNH A 6184 can be referred with confidence to the Pseudasturidae, especially because of the presence of the two characters: large foramen vasculare distale and trochlea metatarsi IV bearing a sehnenhalter (characters 10 and 11 of Mayr, 1998).

However, although BMNH A 6184 and the tarsometatarsus of *Pseudastur macrocephalus* are very much alike (and are certainly from very similar birds), there are a number of subtle differences: in *P. macrocephalus* the distal margin of the shaft is raised (the shaft of BMNH A 6184 is somewhat flatter and wider distal to the foramen vasculare distale; the foramen vasculare distale is more elongate and
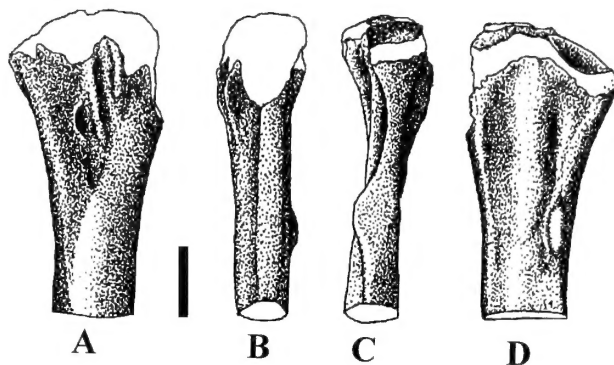

Fig. 3 Proximal end of right tarsometatarsus (BMNH A 5193) referred by Harrison (1982) to the Piciformes ('*Primobucco*' *olsoni* Feduccia & Martin; Primobucconidae). **A**, posterior; **B**, lateral; **C**, medial; **D**, anterior views. Unstippled areas are not preserved. Total length of specimen = 7.82 mm; scale bar = 2 mm. Redrawn after Harrison (1982).

teardrop shaped in *P. macrocephalus* (more circular in BMNH A 6184); and the trochlea metatarsi IV of BMNH A 6184 is wider and more robust. Lateral to the foramen vasculare distale (on the surface of the trochlea) there is a flat and shelf-like angled surface.

On the basis of the Messel material, Mayr (1998) was unable to conclusively demonstrate the fully or faculatively zygodactyl nature of members of the Pseudasturidae (cf. *Pseudastur macrocephalus*): 'whether *Pseudastur macrocephalus* was fully or faculatively zygodactyl is difficult to assess on the basis of the skeletons from Messel known so far'. This is because in all the known Messel specimens, the anterior portion of the trochlea metatarsi IV is obscured as a result of compaction during preservation (Mayr, 1998). On the basis of BMNH A 6184, an entirely uncrushed specimen, it is possible to confirm the observation of Mayr (1998) that members of this extinct clade had developed a fully zygodactyl foot morphology (Fig. 4).

BMNH A 6224 and A 5193 can be tentatively referred to the Pseudasturidae on the basis of comparisons with *Pseudastur macrocephalus* (WDC-C-MG-94). Both of the London Clay specimens are of a similar size and correspond with the proximal tarsometatarsi of WDC-C-MG-94 (although they are slightly larger; see measurements). As in WDC-C-MG-94, the foramina vascularia proximalia are at the same level on the shaft, the inner one being somewhat larger. The hypotarsal areas in the three specimens are identical (although only the crista medialis hypotarsi is seen clearly in WDC-C-MG-94); this protrudes over the fossa infracotylaris dorsalis and the impressio ligamentis collateralis is pronounced in all three specimens.

Harrison (1982) referred BMNH A 5193 (Fig. 3) to the taxon '*Primobucco*' *olsoni* (quotation marks added after Mayr, 1998) within the extinct family Primobucconidae erected by Feduccia & Martin (1976) within the order Piciformes. He noted that 'within that family, it [BMNH A 5193] appears to match in characters and size the corresponding bone of *Primobucco olsoni* Feduccia & Martin, as described and figured by them'. Harrison (1982) provided no further indication of what these characters might be. Referral of this specimen to within the order Piciformes cannot be confirmed with any degree of confidence: although monophyly of the order has been supported on the basis of a number of characters (i.e. zygodactyl foot, type IV flexor tendons, and m. flexor hallucis longus three-headed; Simpson & Cracraft, 1981; Swierczewski & Raikow, 1981; Raikow & Cracraft, 1983), none of these can be confirmed for

Fig. 4 Distal end of left tarsometatarsus (BMNH A 6184) in plantar view. The pointer indicates the laterally retroverted portion of trochlea metatarsi IV (the senhenhalter of Steinbacher, 1935).

BMNH A 5193 since they all refer to the distal portions of the tarsometatarsus. Further, Mayr (1998) commented on the status of '*Primobucco*' *olsoni* and noted that it is likely that the type specimen of this taxon may also be referable to the Pseudasturidae.

CONCLUSIONS

(1)   The referral of a number of new specimens from the London Clay Formation to the extinct landbird clade Pseudasturidae Mayr confirms the fully zygodactyl foot morphology of these birds.

(2)   The recognition of specimens referable to the Pseudasturidae within the fossil bird collections of the London Clay Formation further serves to highlight the compositional similarity seen between this deposit and the roughly contemporaneous deposit of Grube Messel, Germany (see Mayr, 1998). At least in terms of the clades of landbirds, the two deposits are remarkably uniform in their composition (Dyke, 1998) and serve to illustrate the 'settling' of a number of the landbird clades by the time of the earliest Eocene.

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Novocrania, a new name for the genus *Neocrania* Lee & Brunton, 1986 (Brachiopoda, Craniida), preoccupied by *Neocrania* Davis, 1978 (Insecta, Lepidoptera)

DAPHNE E. LEE
Department of Geology, University of Otago, Box 56, Dunedin, New Zealand
**C. H. C. BRUNTON**
Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

David Campbell has brought to our attention (personal communication 9 March 2000) that the generic name *Neocrania* Lee & Brunton, 1986 (Brachiopoda, Craniida) is preoccupied by an insect (Lepidoptera) genus published by Davis, 1978. According to Article 60 of the ICZN rules, we here propose *Novocrania* (from the Latin, *novus*, new, young, recent, and *Crania*, the name given by Retzius, 1781) as replacement name for *Neocrania* Lee & Brunton, 1986, *non Neocrania* Davis, 1978. As required for a replacement name, the type species remains *Crania anomala* Müller, 1776, as in the preoccupied original genus.

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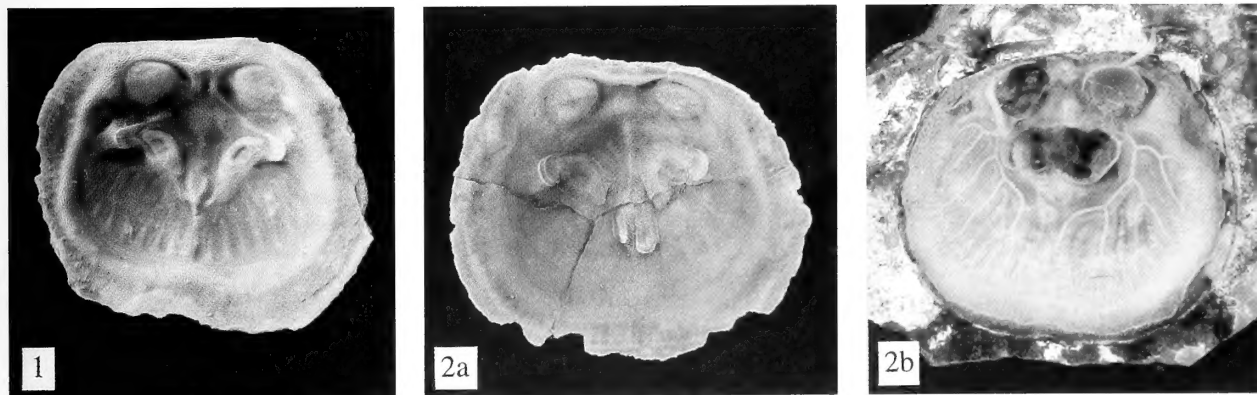
Figs 1, 2 *Novocrania anomala* (Müller). **1,** from the North Atlantic, NHM ZB 124/23, Cuming Collection; previously figured by Reeve (1862: pl. 1, fig. 4); interior of dorsal valve showing the impressions of mantle canals and muscle scars, including the antero-median brachial protractor scars. **2a, b,** from Knähaken, Öresund, Denmark, from waters probably close to those from which Müller's original material was found; NHM ZB 3955; **2a,** interior of dorsal valve showing the muscle scars; **2b,** attached ventral valve with some mantle tissue remaining, showing the mantle canal and the posterior and anterior muscle scars. All figures × 3.

XX (335149)

The Creswellian (Pleistocene) human upper limb remains from Gough's Cave (Somerset, England)

STEVEN E. CHURCHILL

Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27708, USA

SYNOPSIS. The human remains from the Pleistocene deposits in Gough's Cave include more than 25 fragmentary elements from the pectoral girdle and upper limb. These remains are described here, and represent at least three and most likely four individuals (two larger, possibly male individuals and two smaller, possibly female or juvenile individuals). Many of these fragmentary bones show marks made by stone tools, including one element (a right radius) with engraving, suggesting human damage before they were deposited.

INTRODUCTION

The human upper limb remains from the Creswellian levels of Gough's Cave, like those of the lower limb (Trinkaus, this volume), are highly fragmentary. In some cases multiple pieces have been refitted along peri-/post-mortem breaks (the conjoined pieces now being cataloged as a single element), but the assemblage overall remains a fragmentary one, with little possibility of associating pieces by individual. Evidence of human modification of the skeletal elements is abundant (see Cook, 1986; Currant *et al.*, 1989; Andrews & Fernandez-Jalvo, this series of papers), and humans were undoubtedly at least partly responsible for the damage that is characteristic of this assemblage.

The following description provides inventory information (using the current Natural History Museum catalogue numbers [M.54XXX series], followed by an excavation number or numbers), along with observations on the state or preservation and the morphology of each element. Osteometric comparisons were made, where possible, with comparably-aged (*i.e.*, terminal Pleistocene) European fossil humans. The comparative sample derives primarily from Magdalenian/Epigravettian contexts (*ca.* 16 – 10 kya), and includes male specimens Arene Candide 2, 4, 5, 10 and 12, Chancelade 1, Gough's Cave 1, Le Placard 16, Neuessing 2, Oberkassel 1, Rocheriel 1, Romanelli 1, Romito 3, and Veyrier 1, 7 and 9 (Paoli *et al.*, 1980; Vallois, 1941–46; Seligman & Parsons, 1914; Breuil, 1912; Gieseler, 1977; Verworn *et al.*, 1919; Boule & Vallois, 1946; Stasi & Regalia, 1904; Pittard & Sauter, 1945), and female specimens Arene Candide 13 and 14, Bruniquel 24, Cap Blanc 1, Farincourt 1, Oberkassel 2, Romito 4 and St. Germain-la-Rivière 4 (Paoli *et al.*, 1980; Genet-Varcin & Miquel, 1967; Bonin, 1935; Sauter, 1957; Verworn *et al.*, 1919). All comparative data were collected by the author on original specimens.

Five specimens – three claviculae, one humerus and one ulna – had diaphyses reasonably complete to estimate cross-sectional geometric properties. The small number of specimens of each element and a general lack of comparative data combine to limit the conclusions that can be drawn from structural analysis of diaphyseal morphology. The cross-sectional data are thus included merely as a supplement to the morphological descriptions.

Diaphyseal cross-sections were reconstructed from radiographs and external contour moulds for the midshaft (claviculae and humeri)

or mid-proximal (ulnae) diaphyses. Subperiosteal contour moulds were taken perpendicular to the diaphyseal axis, using dental putty moulds (Cuttersil Putty Plus: Heraeus Kulzer Inc.), at 50% (midshaft) or 65% (mid-proximal) of biomechanical length (measured from the distal end). The moulds where photostatically reproduced on paper to provide the subperiosteal (outside) contour of the cross-section. In the case of claviculae, ventral, dorsal, superior and inferior cortical thickness dimensions were measured from superoinferior and dorsoventral radiographs. For humeri and ulnae, anterior, posterior, medial and lateral cortical thickness dimensions were measured from mediolateral and anteroposterior radiographs. Subperiosteal dimensions from the original specimens were compared with those from the radiographs to determine the degree of parallax distortion and thus allow for algebraic correction of cortical thickness measurements. The cortical dimensions were used along with the subperiosteal contour to interpolate the endosteal contour. The resultant cross-sections were manually digitized and geometric properties were computed using a PC-DOS version (Eschman, 1990) of SLICE (Nagurka & Hayes, 1980).

SLICE calculates the total subperiosteal (TA) and cortical (CA) areas, second moments of area about the superoinferior (clavicle) or anteroposterior (humerus and ulna) (I_x) and dorsoventral (clavicle) or mediolateral (humerus and ulna) (I_y) axes, and the maximum (I_{max}) and minimum (I_{min}) second moments of area. Geometric analysis of cross-sections provides measures of the contribution of bone geometry to the resistance of biomechanical loads: in the case of cortical area, to axial compressive and tensile loads; for second moments of area, to bending loads. Medullary area (MA) can be determined from total and cortical areas (MA = TA – CA). The polar moment of area (J, or I_p) is a measure of torsional rigidity and overall strength, and can be determined as the sum of any two perpendicular second moments of area (J = [$I_x + I_y$] = [$I_{max} + I_{min}$]).

In addition to the measures of bone rigidity outlined above, three cross-sectional shape indices were computed to better illustrate the morphology of the Gough's Cave Creswellian upper limb material. The first of these is percent cortical area (%CA = 100*CA/TA), which serves as a simple measure of the degree of cortical occlusion of the medullary space. Ratios of second moments of area provide information about diaphyseal shape (at the location of the cross section) with respect to anatomical axes (I_x/I_y) or with respect to the axis of maximum bending rigidity (I_{max}/I_{min}).

CLAVICULAR REMAINS

M.54053 (M23.1/1) (Fig. 1)
Left
This is a complete clavicle. With the exception of some abrasion and erosion of the sternal end on the inferior margin and to a portion of the superior edge, and some very slight damage to the lateral edge of the acromial articular surface, the bone is in a perfect state of preservation. There is marked curvature to both the medial and lateral ends of the shaft. There is very little torsion to the shaft, except at the very proximal end, such that the long axis of the sternal articulation is oriented at 135° to the horizontal plane of the acromial end. Medially the shaft cross-section forms an isosceles triangle with the base superior, while laterally the shaft is more rectangular in section, with the superoinferior dimension being the smaller.

Fig. 2   Right proximal clavicle, M.54054, natural size. **2A,** superior; **2B,** inferior.

Cutmarks are evident on the medial inferior surface (around the costoclavicular ligament attachment area), near midshaft, and on the anterosuperior margin of the acromial facet (see Andrews & Fernandez-Jalvo, this series of papers).

Along the superior surface, there is very mild rugosity at the insertion area for *M. Sternocleidomastoideus*. There is a weak but clear crest delimiting the superior edge of the *M. pectoralis major* origin on the superoventral margin of the medial third of the shaft. Just lateral of midshaft this crest blends with the origination scar for *M. deltoideus*. Medially the *M. deltoideus* scar is rugose and well defined, laterally the muscle origin is marked by a clear crest superiorly and a rugose tubercle laterally, but the bone surface over most of this part of the origin area is not especially rugose. The insertion area for *M. trapezius* is marked by some smooth tubercles medially (just medial of the level of the conoid tubercle) and some rugosity just mediodorsal of the acromial articular surface. The superior surface of the acromial end is relatively smooth.

On the inferior surface, the origin of *M. sternohyoid* can be seen as a small patch of very slight rugosity. The costoclavicular ligament attachment is marked by a pit with small exostotic projections lining the dorsal edge of the ligament scar. The oval costoclavicular ligament scar is continued laterally as a rugose broad ridge extending roughly 29mm along the inferior shaft. This ridge may mark the inferior edge of *M. pectoralis major*, perhaps including some of the attachment area of *M. subclavius* and the clavipectoral fascia near midshaft. The conoid tubercle is well defined and large, and projects

Fig. 1   Left clavicle, M.54053, natural size. **1A,** superior; **1B,** inferior.

dorsally and inferiorly. The trapezoid line is rugose and well defined. The dorsolateral surface of the acromial end has a number of rugose tubercles, perhaps indicating the attachment of *M. trapezius*.

There are no signs of degenerative changes on the sternal articular surface, while the acromial facet is pitted and vascular, with some very incipient lipping along the inferior border.

M.54054 (GC 89 022) (Fig. 2)
Right

This 108.7mm long fragment represents the proximal end of a right clavicle, preserving the superior portion of the sternal articular surface, most of the corpus laterally to the point of maximum curvature of the proximal shaft, and the superior and dorsal surfaces of the shaft to the proximal part of the *M. deltoideus* origination area (medial of the conoid tubercle). The inferior portion of the sternal end is broken away. In size and shape (including proximal shaft curvature) this specimen matches M.54053, with the exception that in M.54054 the sternal epiphyseal plate is unfused and missing. Oblique cutmarks are evident on the superior surface near the sternal end.

The *M. pectoralis major* appears to have been well developed in this individual. The superior line of attachment of the muscle begins as a projecting but only mildly rugose ridge on the anterosuperior margin of the clavicle just lateral of the sternal articular surface. The muscle attachment area is moderately rugose, and leaves a flattened surface laterally on the anterosuperior shaft that is almost continuous with the medial *M. deltoideus* attachment scar. Only a small portion of the *M. deltoideus* scar is preserved. Inferiorly, the costoclavicular ligament attachment area is a large, very deep and very rugose pit (Fig. 2B). A very clear ridge extends laterally from the costoclavicular ligament pit, marking the inferior extent of the *M. pectoralis major* muscle. There also appears to be a crest for *M. subclavius* extending from this ridge laterally. A tubercle can be seen where the inferior surface of the clavicle is broken, which would be in the area of *M. subclavius* attachment. If this is the antimere to M.54053, it would indicate some asymmetry in muscularity if not robusticity.

M.54055 (GC 87 116) (Fig. 3)
Right

This specimen preserves only the diaphysis of a right clavicle. The bone is preserved medially to the sternal metaphysis just medial of the costoclavicular ligament attachment area, and laterally to the area of the trapezoid line. The bone is fairly slender and gracile, with a moderate curvature to the medial and lateral portions of the shaft. In section, the proximal portion of the shaft is a triangle with height larger than base, more distally the shaft is rectangular with length approaching twice the width. Cutmarks (possibly recent) can be seen on the inferior surface just proximal of the conoid tubercle and on the anterosuperior shaft at the lateral end of the *M. pectoralis major* attachment area.

The anterior surface of the shaft is mildly rugose, but becomes increasingly so laterally past the point of maximum proximal curvature up to the medial end of the *M. deltoideus* origin area. Around mid-shaft the anterior surface is flat and is delimited by a clear crest superiorly, likely demarcating the lateral part of the *M. pectoralis major* origin area, which is separated from the small *M. deltoideus* attachment area by a smooth gap of ca. 10mm. The scar for the deltoid muscle is a small patch of moderately rugose bone on the superior surface of the shaft, with a very thin and small shelf of bone projecting anteriorly. The *M. trapezius* insertion area is smooth.

On the inferior surface, there is an inferiorly projecting tubercle on the proximal end of the bone in the area of the attachment of *M. sternohyoid*. The costoclavicular ligament attachment area is an irregular oval bounded by a crest anteriorly (perhaps for *M. pectoralis*

Fig. 3 Right clavicle, M.54055, natural size. **3A,** superior; **3B** inferior.

major) that gives the attachment area a concave appearance. This crest continues laterally as a blunt ridge, mildly rugose at first but becoming smoother laterally, that continues the length of the proximal shaft. This ridge forms a small sulcus dorsally near the lateral end of the proximal shaft, in the region of the lateral end of the *M. subclavius* attachment. The conoid ligament is well defined, positioned on the very dorsal edge of the inferior surface and projecting directly inferiorly. The trapezoid line appears as an abnormally large tubercle (at least 10.5mm wide by more than 12mm long and projecting 2mm from the inferior surface of the acromial process). In anterior view this tubercle looks like a facet for a pseudoarthrosis with the coracoid, but when viewed from below there is indication of neither an articular surface nor polished bone. This tubercle appears to represent an 'enthesopathic' outgrowth (musculoskeletal stress marker: Hawkey & Merbs, 1995) of bone due to activity or, less likely, a pathological ossification of the trapezoid ligament.

Morphology

The Creswellian-associated claviculae from Gough's Cave represent a minimum of two individuals, a larger, relatively robust individual represented by the left and right claviculae M.54053 and M.54054 and a smaller, somewhat more gracile individual represented by the right clavicle M.54055. The complete left clavicle M.54053 is long and large relative to late Upper Palaeolithic male claviculae, and the right side M.54054 has mid-proximal shaft dimensions that are larger than or approximately equal to the mean values for the male

Table 1   Clavicular dimensions (mm).

Measurement	M.54053	M.54054	M.54055
Maximum length (M-1)	152	–	–
Articular length[a]	146.2	–	–
Conoid length[b]	115.9	–	[98]
Midshaft maximum diameter[c]	13.6	–	11.9
Midshaft minimum diameter[c]	11.0	–	9.1
Midshaft circumference (M-6)	39	–	33
Mid-proximal superoinferior diameter[d]	12.0	14.7	10.6
Mid-proximal anteroposterior diameter[d]	13.0	11.8	8.8
Mid-proximal circumference[d]	42	43	32
Proximal epiphyseal superoinferior diameter[e]	(22)	–	–
Proximal epiphyseal anteroposterior diameter[e]	15.9	–	–
Costal impression mediolateral diameter[f]	17.9	(23.1)	13.8
Costal impression dorsoventral diameter[f]	10.9	10.5	7.3
Conoid superoinferior diameter[g]	14.6	–	12.1
Conoid anteroposterior diameter[g]	17.8	–	13.5
Acromial superoinferior diameter[h]	10.9	–	–
Acromial anteroposterior diameter[h]	19.3	–	–

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.

[a] direct distance between the mid-points of the proximal and distal epiphyses.

[b] direct distance from the mid-point of the proximal epiphysis to the middle of the conoid tubercle.

[c] midshaft determined relative to articular length (midshaft position estimated for M.54055).

[d] taken at mid-conoid length (mid-proximal position estimated for M.54054 and M.54055).

[e] maximum (SI) and minimum (AP) diameters of the proximal epiphysis.

[f] mediolateral and dorsoventral diameters of the costoclavicular ligament attachment area.

[g] taken at the conoid tubercle perpendicular (SI) and parallel (AP) to the superior surface of the bone.

[h] acromial diameters taken perpendicular (SI) and parallel (AP) to the superior surface of the bone.

Table 2   Comparative clavicular osteometrics (mean, SD, n).

Right claviculae	M.54054	M.54055	U.P. ♂	U.P. ♀
Conoid length	–	[98]	111.3, 7.9, 8	103.6, 7.6, 4
Mid-proximal SI diameter	14.7	10.6	11.9, 1.9, 8	9.8, 0.6, 5
Mid-proximal AP diameter	11.8	8.8	11.7, 1.0, 8	10.2, 1.0, 5
Conoid SI diameter	–	12.1	11.7, 2.2, 8	10.4, 1.2, 6
Conoid AP diameter	–	13.5	17.5, 2.0, 8	15.4, 2.1, 6
Left claviculae	M.54053		U.P. ♂	U.P. ♀
Maximum length	152		145, 8.9, 8	128, –, 2
Articular length	146.2		141.8, 8.7, 8	125.6, –, 2
Conoid length	115.9		112.2, 9.5, 9	100.1, 5.8, 3
Mid-proximal SI diameter	12.0		11.0, 1.6, 12	9.7, 0.5, 5
Mid-proximal AP diameter	13.0		11.7, 0.8, 12	10.1, 1.2, 5
Conoid SI diameter	14.6		11.3, 2.0, 11	10.7, 0.4, 5
Conoid AP diameter	17.8		15.9, 2.0, 11	13.8, 1.3, 5

All measurements are in millimeters and are defined in Table 1.

comparative sample (Table 2). Both claviculae exhibit moderate to heavy rugosity of muscle scars and ligament attachment areas. M.54053 has greater mid-shaft cross-sectional strength measures than the left claviculae of the male specimens Gough's Cave 1 and Rocheriel 1 (Table 3). The right clavicle M.54054 is larger in some cross-sectional strength values than Gough's Cave 1 and smaller in others, likely reflecting shape differences related to differences in mechanical loading (and hence behavioral) histories of the collar bone in these two individuals. On the basis of size, robusticity and muscular rugosity, it seems reasonable to conclude that M.54053 and M.54054 derived from male individuals, and that they likely belonged to the same individual (see above). If they are indeed antimeres, the greater development of the *M. pectoralis major* origin scar and costoclavicular ligament scars on the right side would suggest a considerable degree of bilateral asymmetry in limb use and a right hand-dominant individual. Based on the different stages of sternal epiphyseal fusion in

the two sides, and again assuming both claviculae derive from the same person, this individual was probably between the ages of 18 and 25 at the time of death (Williams & Warwick, 1980).

The right clavicle M.54055 is much more gracile, in both external and cross-sectional dimensions (Tables 2 and 3). In overall size and shape this specimen compares most favourably with females of the comparative sample and thus probably represents a female, although the possibility that the specimen represents a juvenile male cannot be ruled out. Although the bone is relatively lightly constructed, the muscle scars (especially that of *M. deltoideus*) are fairly well defined and the costoclavicular ligament attachment area is rugose. The existence of a (possible) musculoskeletal stress marker at the attachment of the trapezoid ligament suggests that this individual engaged in a repetitive motion involving humeral abduction, since this motion engenders scapular rotation and stresses the acromioclavicular ligaments.

Table 3 Mid-shaft clavicular cross-sectional properties.

Right claviculae	M.54054	M.54055	GC1[a]
Total area (TA) (mm^2)	135.0	76.5	124.9
Cortical area (CA) (mm^2)	83.6	56.5	87.3
Medullary area (MA) (mm^2)	51.4	20.0	37.6
SI second moment of area (I_x) (mm^4)	1502.3	497.7	1319.8
DV second moment of area (I_y) (mm^4)	1026.3	387.2	1154.2
Maximum 2nd moment of area (I_{max}) (mm^4)	1502.5	540.6	1752.1
Minimum 2nd moment of area (I_{min}) (mm^4)	1026.2	344.3	721.9
Polar moment of area (J) (mm^4)	2528.7	884.9	2474.0
Percent cortical area (%CA)	61.9	73.9	69.9
I_x/I_y	1.46	1.28	1.14
I_{max}/I_{min}	1.46	1.57	2.43
Left claviculae	M.54053	GC1[a]	Roch1[b]
Total area (TA) (mm^2)	126.4	118.9	98.6
Cortical area (CA) (mm^2)	94.6	73.9	69.8
Medullary area (MA) (mm^2)	31.8	45.0	28.8
SI second moment of area (I_x) (mm^4)	1014.3	999.6	654.4
DV second moment of area (I_y) (mm^4)	1395.8	1084.4	784.1
Maximum 2nd moment of area (I_{max}) (mm^4)	1408.8	1505.1	824.6
Minimum 2nd moment of area (I_{min}) (mm^4)	1001.3	578.9	613.9
Polar moment of area (J) (mm^4)	2410.1	2084.0	1438.5
Percent cortical area (%CA)	74.8	62.2	70.8
I_x/I_y	0.73	0.92	0.83
I_{max}/I_{min}	1.41	2.60	1.34

[a] Gough's Cave 1.
[b] Rocheriel 1.

SCAPULAR REMAINS

M.54056 (M23.1/2 (1959)) (Figs 4–6)
Right
This specimen preserves a portion of the body, spine, coracoid process, axillary border and glenoid fossa of a right scapula (Fig. 4). The fragment measures ca. 123mm superoinferiorly by ca. 76mm mediolaterally. The spine is missing the acromion and all of its upper (superodorsal) border from the 'waist' (the point of minimum thickness between the acromion and the flared attachment for *M. deltoideus*) medially. Laterally the root of the spine is not preserved, nor is any of the vertebral border of the body. The superior surface of the spine is recently altered (from removal of a bone sample for direct dating), and most of the supraspinous fossa (including the superior angle) is absent from the suprascapular notch medially. Only the root of the coracoid is preserved, but virtually all of the glenoid fossa is intact (there is some damage or erosion to the ventroinferior margin). The axillary border is complete down to the distal origin of *M. teres major*.

The scapula exhibits numerous cutmarks. There is a series of obliquely oriented marks on the dorsal surface of the body in the infraspinous fossa, a few around the inferior ventral surface of the root of the coracoid and around the area of the supraglenoid tubercle, numerous marks running transversely across the dorsal pillar of the axillary border, and a series of superoinferiorly oriented marks on the dorsal surface at the *M. teres major* origin.

The glenoid fossa is a very broad piriform shape (Fig. 5). The articular surface is oriented slightly cranially and dorsally. There is a small (incipient) central pit evident on the articular surface. The attachment for the glenoid labrum can be clearly seen along most of the articular margin, especially so along the dorsal edge. No degenerative changes are evident on the articular surface.

There is only a small, smooth projection representing the supraglenoid tubercle, with a broad, diffuse attachment area (for the coracohumeral ligament and for the long head of *M. biceps brachii* ventrally) extending for 10–15mm along the superior dorsal margin of the glenoid fossa. The infraglenoid tubercle begins as a broad triangle whose base is positioned along the dorsal-most part of the inferior margin of the fossa. The tubercle is well developed and rugose. The tubercle continues distally as a high, thin dorsal pillar that forms the lateral edge of the axillary border. There is also a distinct tubercle on the ventroinferior margin of the glenoid, perhaps indicating a separate muscle slip from *M. triceps brachii*.

The axillary border exhibits a ventral sulcus (sulcus ventroaxillaris or sulcus axillaris subscapularis: Gorjanovic-Kramberger, 1914; von Eickstedt, 1925). The dorsal pillar (axillary scapular buttress on the dorsal scapular body: Smith, 1976) forms the extreme lateral edge of the border (Fig. 6). The groove for the circumflex scapular artery is clear. The axillary crest (crista medioaxillaris: Vallois, 1932) is lost superiorly in the rugosity of the infraglenoid tubercle, but can be made out on the dorsal pillar just superior of the groove for the circumflex scapular artery, and can be seen running directly inferiorly along the dorsal edge of the border. The crest is positioned, in its entirety, along the ventral edge of the dorsal pillar. The ventral pillar (ventral axillary scapular buttress) is strongly developed but is medially positioned (superiorly it begins below the middle of the coracoid root, inferiorly it converges with the dorsal pillar at the level of the *M. teres major* origin), and there is a wide, moderately deep ventral sulcus between the pillars.

The *M. teres minor* imprint is distinct (both superior and inferior areas) and a slight crest delineates the attachment area medially. The *M. teres major* origin area is preserved as a flattened facet that looks as if it continued laterally as a projection from the axillary border (postmortem breakage in this region makes evaluation of the morphology difficult). Some rugosity is evident along the *M. deltoideus* attachment area of the preserved portion of the spine.

This scapula belonged to an adult. The subcoracoid and inferior glenoid fossa rim secondary centres of ossification are both fully fused and the growth lines obliterated (both centres appear around
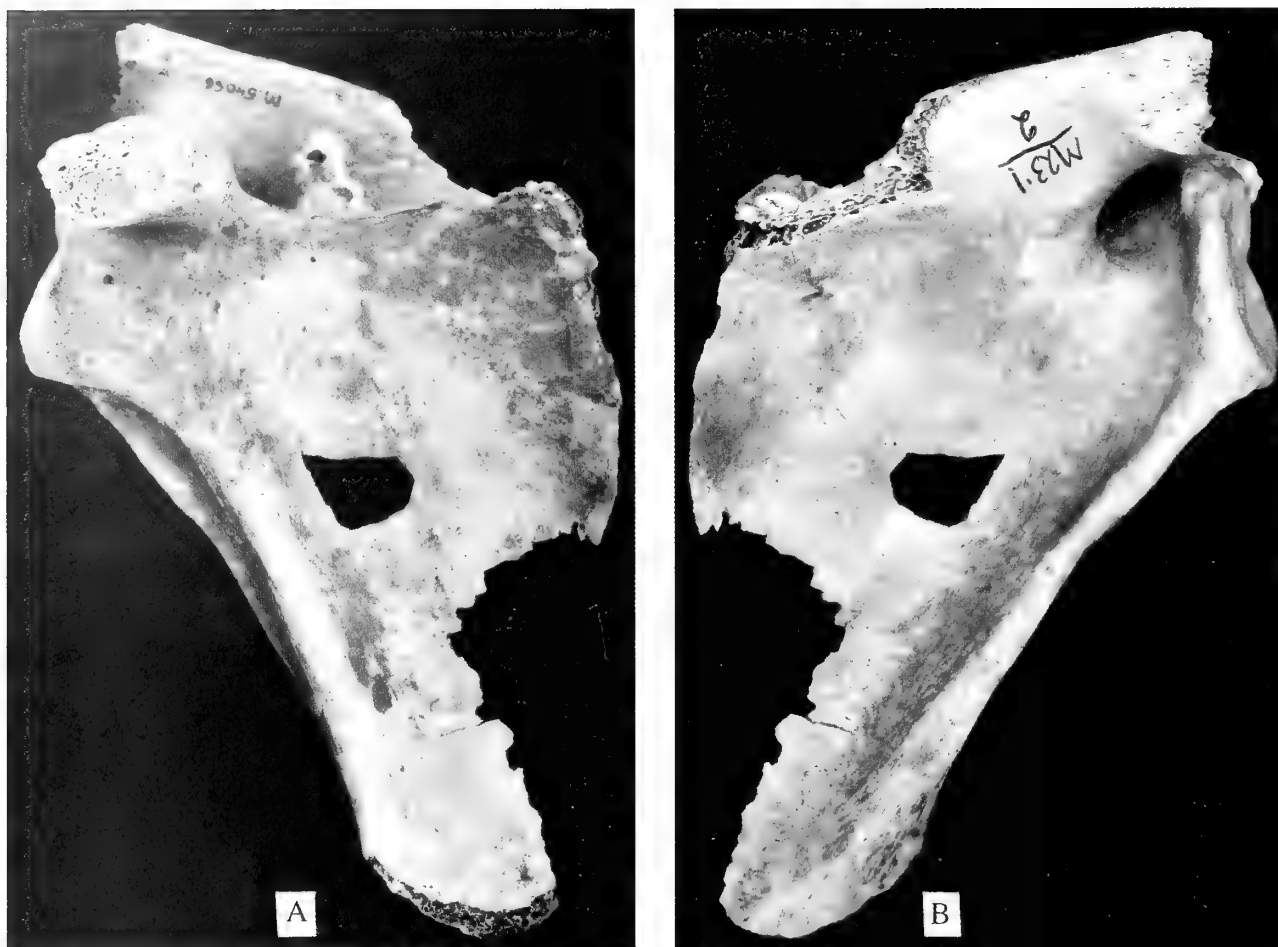
Fig. 4   Right scapula, M.54056, natural size. **4A,** ventral; **4B,** dorsal.

puberty and fuse by around age 20: Williams & Warwick, 1980). On the basis of size and morphology, this specimen is likely to have been the antimere of M.54057 (see below).

M.54057 (GC 87 266/89 012) (Figs 7, 8)
Left

Two fragments (GC 87 266 and 89 012) that join to form a portion of a left scapula, preserve the glenoid fossa, axillary border, body, and spine (Fig. 7). The total superoinferior length of the fragment is ca. 80mm and the mediolateral width is roughly 95mm. The spine continues medially to the vertebral border, but it is damaged along its superior margin, and the junction of the spine and vertebral border is not complete. The acromion is missing and the coracoid process is broken off at the root. The axillary border is complete and most of the body is present. Matrix adheres to parts of the body, spine and inferior axillary border. Scratches (perhaps cutmarks) are visible on the body, around the root of the spine, and on the dorsal aspect of the axillary border.

In size and morphology this specimen looks to be the antimere of M.54056. The glenoid fossa forms a broad piriform (Fig. 8), although not quite as dramatically as in the right scapula M.54056, and in other aspects of the morphology of the glenoid fossa and the supraglenoid tubercle, infraglenoid tubercle, axillary border and muscle markings this specimen is virtually identical to that of

M.54056 (with the single exception that there does not appear to be a second tubercle for the long head of *M. triceps brachii* on the inferoventral margin of the glenoid fossa).

As with M.54056, this scapula clearly belonged to an adult. The subcoracoid and inferior glenoid rim secondary centres of ossification

Table 4   Scapular dimensions (mm).

Measurement	M.54056	M.54057	M.54058
Morphological length (M-2)	–	(92.8)	–
Basal spinous length (M-8)	–	(75.2)	–
Mid-axillary border thickness[a]	(11.7)	–	9.8
Spino-glenoid angle (M-22)	88°	105°	(101°)
Axillo-glenoid angle (M-17)	48°	55°	38°
Axillo-spinal angle (M-16)	56°	50°	63°
Glenoid maximum length (M-12)	31.3	31.7	33.7
Glenoid maximum breadth (M-13)	26.9	25.4	(23.2)
Glenoid articular length[b]	28.0	29.5	30.8
Glenoid articular breadth[b]	25.2	24.3	23.1

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.
[a] dorsoventral diameter of the mid-axillary border, including dorsal and ventral pillars as present.
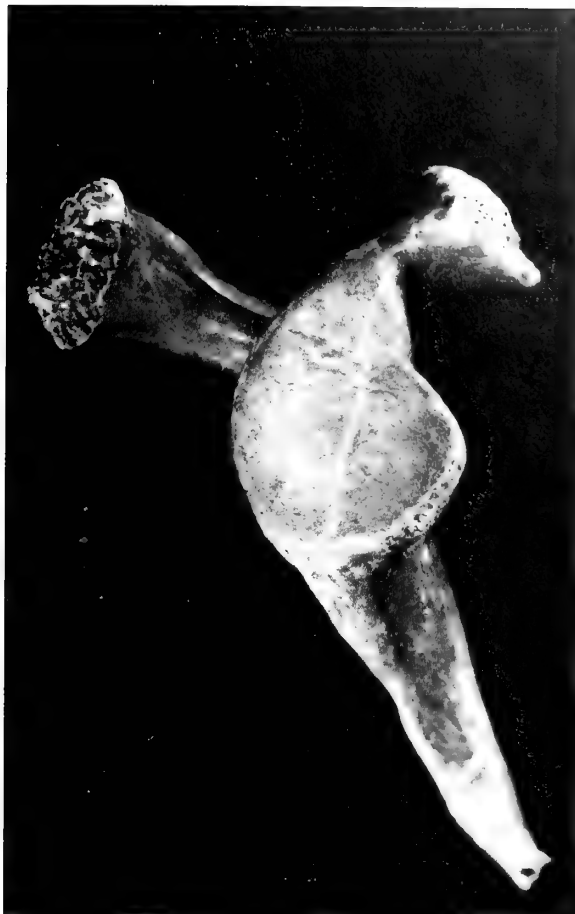[b] Glenoid fossa length and breadth taken across the internal margins of the glenoid labrum attachment.

Fig. 5 Right scapula, M.54056, glenoid fossa in lateral view. 1.25x natural size.

are both fully fused and their growth lines are obliterated, indicating an age in the third decade or older (Williams & Warwick, 1980).

M.54058 (GC 1.1/38) (Fig. 9)
Left

This is a fragment of a left scapula, preserving most of the glenoid fossa (with damage only to the ventroinferior margin), the superior half of the axillary border, the lateral root of the spine, and the root of the coracoid process (Fig. 9). The fragment measures 89.6mm superoinferiorly and 57.0mm mediolaterally. Transversely oriented cutmarks can be seen on the axillary border.

The glenoid fossa is piriform in shape. The attachment of the glenoid labrum can be seen as a clear ridge along most of the margin of the articular surface. There is no evidence of degenerative changes to the joint surface, nor is there any indication of a central pit. The supraglenoid tubercle is small. There is a small, thin crest extending from the supraglenoid tubercle superiorly along the coracoid process, perhaps demarking the attachment area of the coracohumeral ligament. The infraglenoid tuberosity is large and long in the superoinferior direction (ca. 21mm) and comes off the inferodorsal aspect of the glenoid fossa rim. The infraglenoid tubercle is well developed and the entire surface of the tubercle is rugose. The axillary crest (crista medioaxillaris) runs directly inferiorly, maintaining its position along the dorsal part of the border until it reaches the broken edge of the border (ca. 55mm below the glenoid fossa

Fig. 6 Right scapula, M.54056, axillary border in lateral view. Natural size.

rim). The ventral pillar (ventral scapular axillary buttress) is well developed, broad and rounded, and forms a distinct, moderately deep ventral sulcus anterior of the axillary crest. The dorsal pillar (dorsal scapular axillary buttress) is thin and projecting, and is somewhat more laterally placed than the ventral pillar. The dorsal pillar is separated from the dorsal margin of the infraglenoid tubercle proximally by a clear sulcus (but the sulcus is evident only in the region of the infraglenoid tubercle). It then develops as a thin, high ridge that stops roughly 16mm inferiorly at the groove for the scapular circumflex artery. The intersection of the scapular circumflex artery and the axillary border is positioned relatively superiorly in this specimen. Below the groove the dorsal pillar is broader and forms the dorsal edge of the border.

The 'waist' of the superior border of the spine is preserved, as well as the superior surface another 37mm laterally. Fine matrix and sand adheres to the spine, nevertheless it is clear that the *Mm. deltoideus* and *trapezius* markings are not overly rugose. The scapular notch is very broad, the superior edge of the body forming an angle of about 110° with the medial edge of the coracoid process. The attachment
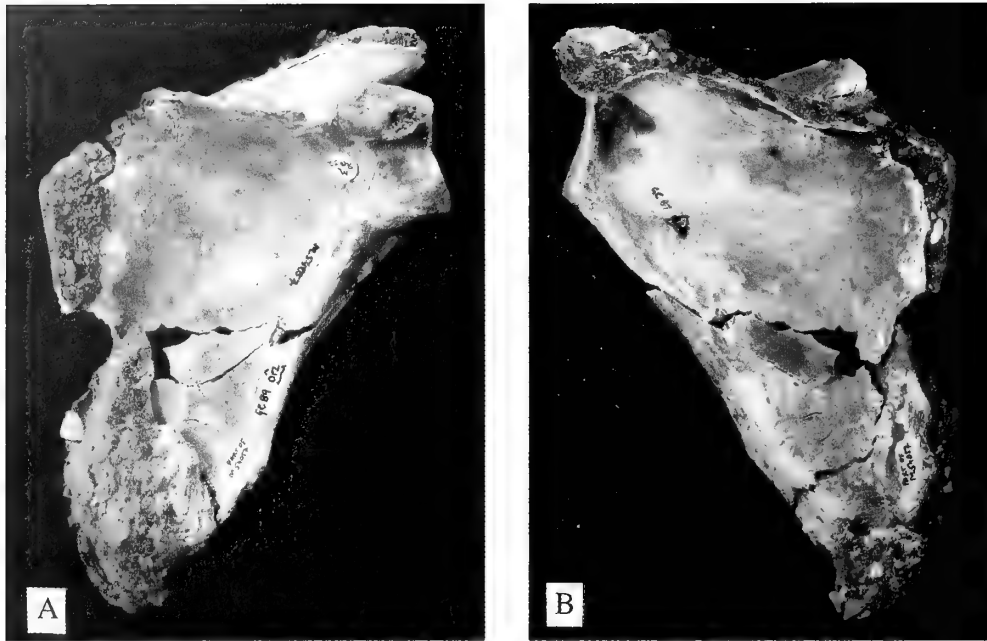
Fig. 7   Left scapula, M.54057, 0.5x natural size. **7A,** ventral; **7B** dorsal.

Fig. 8   Left scapula, M.54057, glenoid fossa in lateral view. Natural size.

area of the conoid ligament can be clearly seen as a smooth facet on the medial superior surface of the coracoid process.

The scapula was that of an adult. The subcoracoid and inferior glenoid fossa rim secondary centres of ossification are both fully fused and the growth lines are obliterated.

M.54059 (GC No. 7) (Fig. 10)
Left
This is a fragment of the lateral root and spine, plus portions of the body, of a left scapula (Fig. 10). The superior portion of the spine is missing and only the root is preserved. The total length of the fragment is 70.8mm superoinferiorly by 37.2mm dorsoventrally.

The scapular notch is preserved and forms a very open semicircle (with an angle of about 116° between the tangents to the two sides). The lateral edge of the notch is horizontal and the medial edge rises relatively steeply towards the superior angle. The notch is positioned close to the lateral root of the spine, and there is virtually no supraspinatus fossa in this specimen, at least on the lateral half of the scapula. The base of the glenoid is narrow ventrodorsally, and there is no indication of the superior end of the ventral pillar in the preserved portion. The subscapular surface abounds with scratch marks – perhaps of recent origin. Cutmarks are also visible on the lateral root of the spine.

Morphology

The scapular fragments from the Creswellian level of Gough's Cave represent a minimum of three individuals. The right and left scapulae M.54056 and M.54057 are morphologically very similar and are likely to derive from the same individual. Based on the overall size of these scapulae this individual was probably male, and judging from the degree of fusion of the observable secondary centres of ossification in the right-side scapula, he was over the age of twenty at the time of death. The left scapular fragment M.54058 also appears to have derived from a relatively large individual, and may likewise represent a male. Again judging from the degree of development of
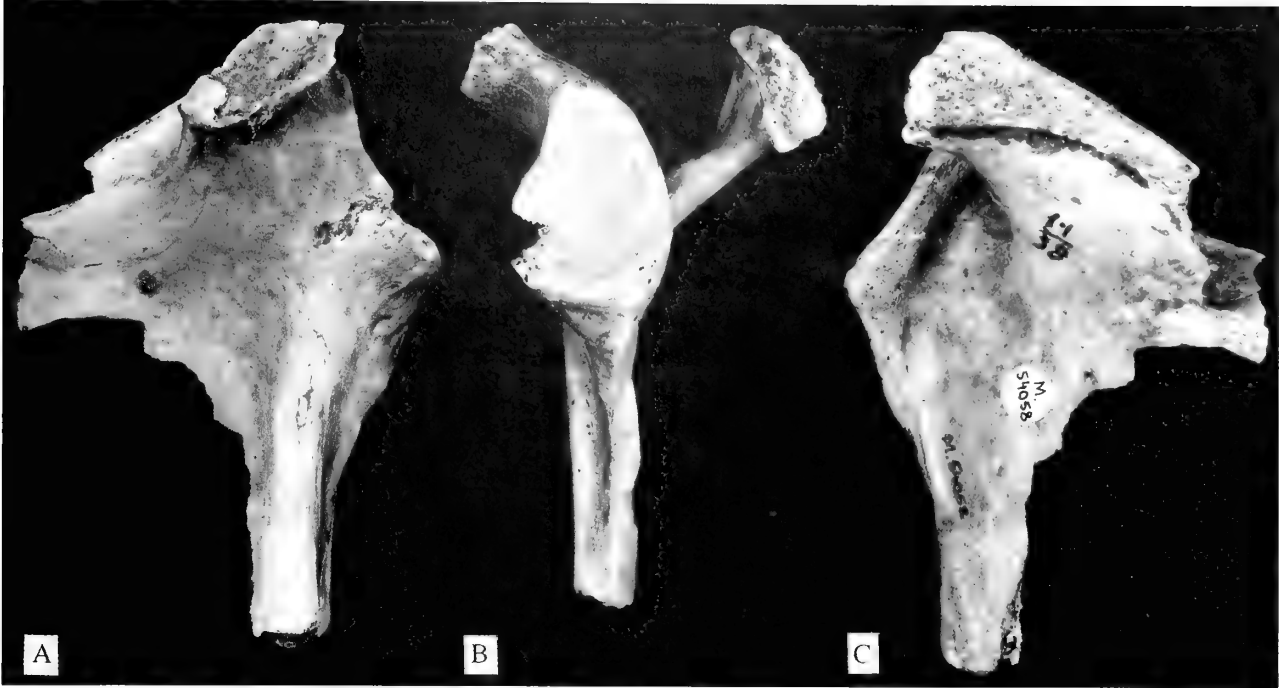
Fig. 9 Left scapula, M.54058, 0.9x natural size. **9A,** ventral; **9B,** lateral; **9C,** dorsal.

Fig. 10 Left scapula, M.54059, natural size. **10A,** ventral; **10B,** dorsal.

secondary growth centres, this individual was also an adult. The left scapula M.54059 appears to have come from a smaller individual, perhaps either a female or a juvenile male.

All three of the preserved glenoid fossae have articular surfaces that are wide relative to their height (Table 5), especially those of M.54056 and M.54057. These two specimens have glenoid indices (100 × articular breadth/articular height) more than five (M.54056) and three (M.54057) standard deviations above the Upper Palaeolithic male mean index values. It is apparent from a comparison of their articular dimensions with those of other Upper Palaeolithic-associated fossils (Table 5) that these inflated index values are due to the relative superoinferior shortness of their glenoid articular surfaces.

Stringer (1985) saw the left scapula M.54058 as possessing a bisulcate axillary border, a feature that is fairly common in Upper Palaeolithic specimens. This specimen does exhibit, in addition to a ventrally positioned sulcus, a sulcus dorsal of the infraglenoid tubercle and proximal axillary crest. It is evident however that the dorsal sulcus does not extend distally more than a centimeter below the infraglenoid tubercle, and for this reason I think the specimen is

Table 5 Comparative scapular glenoid fossa articular dimensions.

	Articular length	Articular breadth	Glenoid Index[a]
M.54056 (right)	28.0	25.2	90.0
M.54057 (left)	29.5	24.3	82.4
M.54058 (left)	30.8	23.1	75.0
U.P. males			
right	36.1 ± 2.3 (6)	25.8 ± 2.2 (5)	72.3 ± 2.6 (5)
left	36.3 ± 1.2 (8)	25.6 ± 1.3 (7)	70.2 ± 3.5 (7)
U.P. females			
right	33.1 ± 1.1 (4)	23.7 ± 1.6 (4)	71.7 ± 5.5 (4)
left	33.2 ± 1.1 (4)	23.4 ± 0.8 (4)	70.5 ± 2.4 (4)

All measurements are in millimeters and are defined in Table 4
[a] Glenoid index = (articular breadth/articular length) × 100

Fig. 11   Gough's Cave humeral assemblage, anterior view, 0.5x natural size. From left to right: M.54062 (left humerus), M.54063 (left humerus), M.54060 (right humerus), M.54061 (right humerus).

perhaps better considered as possessing a ventral sulcus. The other preserved axillary borders exhibit well-developed ventral sulci as well. In a small sample of late Upper Palaeolithic specimens (n=17), Churchill (1994) found roughly equal proportions of ventral sulcate (53% of individuals) and bisulcate (47% of individuals) scapulae.

HUMERAL REMAINS

M.54060 (GC 1950–51, Level 12) (Fig. 11)
Right
This is a 96mm long fragment of a right humeral diaphysis, preserving only the ventrolateral surface (Fig. 11). The distal end of a relatively smooth deltoid tuberosity is preserved. In the vicinity of midshaft (at the distal end of the deltoid tuberosity) the lateral cortical thickness is 4.1mm.

M.54061 (GC 86 18/21) (Figs 11, 12)
Right
These are two diaphyseal fragments that conjoin to form a 180.9mm long portion of a right humeral shaft (Figs 11, 12). The preserved

Table 6   Dimensions (mm) of humeral fragment M.54061.

Midshaft maximum diameter (M-5)	(18.7) (midshaft location estimated)
Midshaft minimum diameter (M-6)	(15.4) (midshaft location estimated)
Midshaft circumference (M-7a)	[57] (midshaft location estimated)
Deltoid tuberosity width[a]	(6.9)

[a] distance between the apices of the delimiting crests of the tuberosity taken at 5/12's of humeral maximum length, following Endo (1971). In this case, the location of 5/12's maximum length was estimated
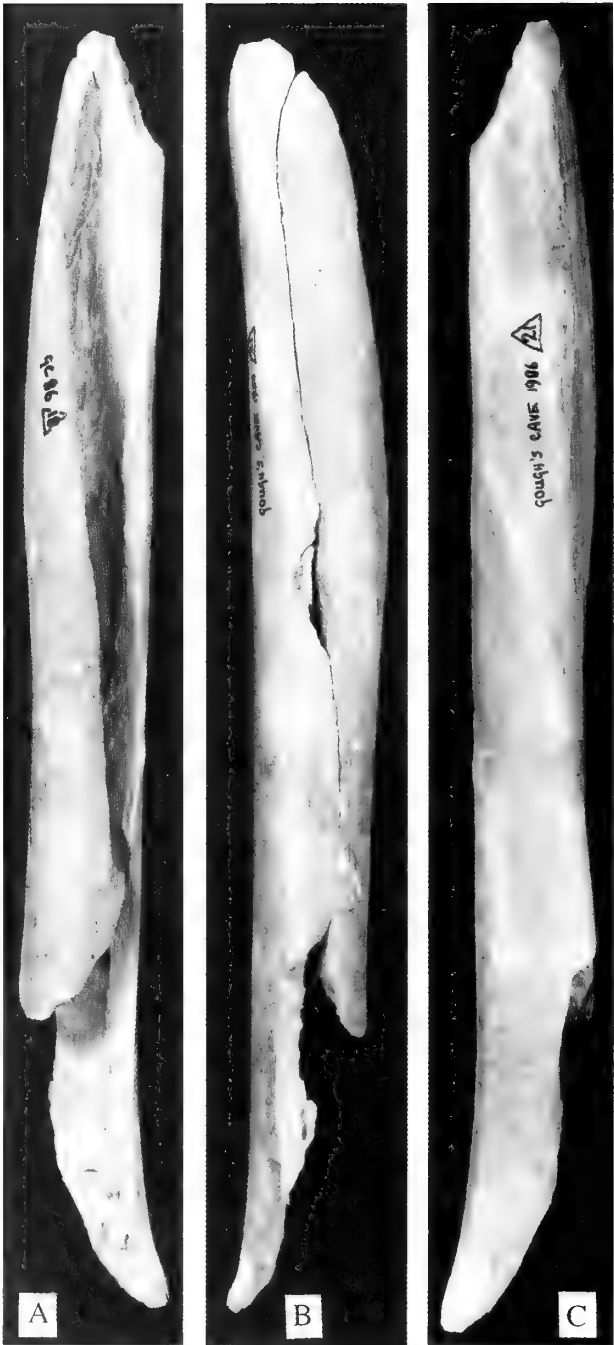
Fig. 12   Right humerus, M.54061, natural size. **12A,** anterior; **12B,** lateral; **12C,** posterior.

portion extends from just proximal of the proximal end of the lateral crest of the deltoid tuberosity to the distal shaft somewhere proximal of the olecranon fossa. The shaft is missing its medial surface for the entire length of the fragment, most of its anterior surface (preserving only the distal portion), and most of its anteromedial surface (preserving only the proximal portion).

The fragment is relatively small and gracile (Table 6), and the preserved muscle scar (*M. deltoideus*) is neither large nor rugose. Both crests of the deltoid tuberosity have faint muscle impressions.

The deltoid tuberosity appears to have been two-crested, with the crests being fairly close together.

M.54062 (GC 87 12/4) (Fig. 11)
Left

This is a 179.5mm long fragment of diaphysis of a left humerus. The bone is preserved from the anatomical neck proximally to the mid-distal shaft (in the vicinity of shaft minimum circumference) distally, with only the dorsomedial surface preserved. The bone is uniformly weathered and has a series of small marks (perhaps cutmarks) along the medial surface of the distal shaft.

The nutrient foramen is preserved on the distal medial surface. A part of the groove for the radial nerve is preserved, as is the proximal portion of the ridge for *M. coracobrachialis*. The *M. coracobrachialis* insertion is non-rugose. The dorso-lateral edge of the lateral ridge of *M. deltoideus* is visible along the lateral edge of the fragment. The preserved part of the deltoid tuberosity is non-rugose. The cortical bone is not markedly thick (at the mid-distal diaphysis, the medial cortical thickness measures 2.8mm and the dorsal thickness is 3.2mm). In overall size and morphology, this specimen could equally well have been the antimere of either M.54060 or M.54061.

M.54063 (GC Level 14) (Fig. 11)
Left

This is a 118.9mm long fragment of the diaphysis of a left humerus. The fragment preserves only the dorsomedial surface of the shaft from the region of the surgical neck (the proximal shaft begins to flare medially very mildly) proximally to the region around the nutrient foramen (and the proximal end of the *M. coracobrachialis* insertion) distally. This fragment preserves much of the same regions as the left humeral fragment M.54062 (see above), and therefore they obviously derive from two different individuals. Numerous cutmarks can be seen on the proximal medial surface, and a few cutmarks can also be seen overlying the *M. coracobrachialis* insertion scar.

A portion of the lateral ridge of the deltoid tuberosity is preserved in this specimen, and is only mildly rugose. The *M. coracobrachialis* scar is non-rugose. In the mid-distal shaft (in the vicinity of shaft minimum circumference) the medial cortex is 4.0mm thick, dorsally it is 4.6mm thick.

M.54064 (GC 87 153 A) (not figured)
This is a 28.8mm long by 25.4mm wide (maximum) triangular-shaped and mildly curved piece of diaphyseal bone. The cortical bone is thin (1.3mm at the edge) but the trabecular bone filling the internal (concave) surface is thick (9.1mm at its thickest point). It appears to represent a portion of the medial surface of the anatomical neck of a humerus.

M.54065 (GC 86 19) (not figured)
This specimen consists of two diaphyseal fragments of a larger long bone, possibly a humerus. The fragments are joined by matrix, and matrix adheres to much of the external surface of one of the fragments. One of the fragments is tubular in shape and is 54.6mm long by 19.2 mm wide. The exposed external surface is slightly weathered, and one end of the internal surface shows some slight trabeculation (the other end is filled with matrix). The cortical bone at one edge is 3.1mm thick.

The second fragment is 75.0mm long by 14.2mm at its widest. It is not certain that this second fragment derives from the same bone as the first, and it is even questionable as to whether it is human.

Morphology

The humeral remains from this assemblage represent a minimum of three individuals. Two relatively small people are represented by the right-side humeral fragments M.54060 and M.54061. Both of these specimens preserve the distal portion of the deltoid tuberosity, and in both the muscle scar is non-rugose. The left-side fragment M.54062 also appears to derive from a smaller individual and also has a non-rugose deltoid tuberosity. This latter specimen could reasonably be associated with either of the right-side fragments. The left humeral fragment M.54063 clearly derives from a larger individual, one with mild rugosity of the deltoid tuberosity, and is unlikely to be the antimere of either of the right-side fragments, thus denoting a third individual.

Little can be said about the morphology of the Creswellian-associated humeri from Gough's Cave. In midshaft cross-sectional properties, the right-side M.54061 is well below even the Upper Palaeolithic female sample means in strength measures (Table 7), suggesting that this element may have belonged to a female or juvenile male. This single specimen also has, judging from the I_x/I_y ratio, a midshaft cross-section that was more resistant to bending in the anteroposterior plane than bending in the mediolateral plane, compared to humeri in the reference sample that are more nearly equal in resistance to bending moments in both planes (Table 7).

ULNAR REMAINS

M.54066 (GC 87 202, 243, 119c) (Figs 13, 14)
Right

This specimen is composed of six fragments that make up most of a right ulna (Fig. 13). Based on size and morphology, this specimen may be the antimere of M.54067 (see below). The total length of the rejoined fragment is ca. 220mm. Preservation of the two pieces making up the proximal end is very good (there is no erosion or weathering, only peri-/post-mortem breakage damage), whereas the fragments comprising the shaft are more heavily weathered. The proximal end is complete (save for the inferior half of the radial notch and the subjacent diaphysis) distally to the base of the coronoid

Table 7 Comparative humeral midshaft cross-sectional geometric properties (mean, SD, n).

	M.54061	U.P.♂	U.P.♀	Total U.P.
Total area (TA) (mm²)	220.0	334.5, 35.2, 10	271.0, 23.7, 6	309.3, 41.7, 18
Cortical area (CA) (mm²)	170.6	242.8, 44.5, 10	191.1, 44.8, 6	224.5, 47.7, 18
Medullary area (MA) (mm²)	49.4	91.7, 26.0, 10	79.8, 21.6, 6	84.7, 24.4, 18
AP 2nd moment of area (I_x) (mm⁴)	4626.1	8310.6, 1960.1, 10	5845.3, 1327.6, 6	7324.2, 1991.3, 18
ML 2nd moment of area (I_y) (mm⁴)	2978.5	8917.5, 2281.0, 10	5314.1, 1575.6, 6	7478.2, 2536.0, 18
Max. 2nd moment of area (I_{max}) (mm⁴)	4638.8	9246.5, 2353.5, 6	7432.4, 3166.8, 3	8476.8, 2511.9, 10
Min. 2nd moment of area (I_{min}) (mm⁴)	2965.7	5762.0, 941.9, 6	4211.7, 1262.3, 3	5286.1, 1182.3, 10
Polar 2nd moment of area (J) (mm⁴)	7604.5	17228.2, 4156.4, 10	11159.4, 2807.0, 6	14802.5, 4459.3, 18
Percent cortical area (%CA)	77.5	72.2, 8.5, 10	69.9, 9.5, 6	72.1, 8.6, 18
I_x/I_y	1.55	0.94, 0.09, 10	1.12, 0.17, 6	1.01, 0.14, 18
I_{max}/I_{min}	1.56	1.59, 0.27, 6	1.75, 0.46, 3	1.61, 0.33, 10

Fig. 13   Right ulna, M.54066, 0.5x natural size. **13A,** anterior; **13B,** lateral; **13C,** posterior.

process on the volar surface. The dorsal and medial surfaces are complete distally to well past midshaft. Only portions of the volar surface of the shaft are preserved. The lateral surface of the shaft is the best preserved, and is almost completely represented from the

proximal end down to the level of the *M. pronator quadratus* crest distally.

The trochlear notch opens anteroproximally (the coronoid process is much higher than the olecranon) (Table 8 and Fig. 14). There is a distinct ridge separating the coronoid and olecranon articular surfaces in the trochlear notch, and there appears to be a small outgrowth of bone just distal of this ridge (on the coronoid articular surface) near the centre of the trochlear notch. There is no indication of degenerative changes to any of the proximal articular surfaces (including the preserved portion of the radial notch).

The proximal surface of the olecranon process is not very rugose, but vertical striations can be seen on the dorsal margin along the *M. triceps brachii* insertion. The area of the *M. anconeus* insertion is weathered and broken, but what is preserved of the muscle scar is non-rugose. The morphology of the proximal *M. supinator* crest cannot be evaluated because of damage to the medial shaft below the radial notch, but this muscle often extends distally well below the level of the *M. brachialis* scar and may overlap the proximal end of the interosseus crest. In the case of M.54066, the distal portion of the muscle attachment can be seen on the proximal shaft, where it is slight but clear, indicating a moderate-to-strong development of the supinator muscle. Only the distal half of the *M. brachialis* scar is preserved, which appears as a well defined, raised scar with clear borders. There is a thin yet clear crest for *M. pronator teres*, but no clear origin area for the ulnar head of *M. flexor digitorum superficialis* can be seen.

More distally, the interosseus crest is a clear, sharp line that diminishes around midshaft and then picks up again on the distal-most part of the fragment as a broader, rugose line. There is a pronounced medial deviation of the shaft at the level of the *M. brachialis* scar, but this may be a function of post-mortem damage and reconstruction of the shaft from numerous fragments. The cortical bone thickness in the proximal shaft (at the level of the beginning of the interosseus crest) is 2.0mm, while in the distal shaft (at the level of the *M. pronator quadratus* crest) it is 2.3mm thick.

M.54067 (GC 87 226 A) (Fig. 15)
Left

This is a proximal left ulna, with a total length of 58.1mm. This may represent the antimere of the right side ulna M.54066 (see above), and may come from the same bone as M.54068 (see below). Only the

Table 8   Ulnar dimensions (mm).

	M.54066	M.54067	M.54069
Olecranon length (M-8)	20.8	18.2	–
Olecranon height (M-7)	24.4	(25)	–
Olecranon breadth (M-6)	26.3	25.2	
Trochlear notch chord (M-7(1))	23.7		–
Coronoid height[a]	37.1	–	–
Radial facet maximum diameter[b]	(>15)	–	–
Radial facet minimum diameter[b]	[9.5]	–	–
Diaphyseal sagittal trochlear angle (M-15a)	15°	–	
Proximal anteroposterior diameter[c]	18.1	–	14.7
Proximal transverse diameter[c]	18.9	–	11.3
Proximal circumference[c]	–	–	45
Crest anteroposterior diameter (M-11)	18.9	18.1	–
Crest mediolateral diameter (M-12)	21.6	21.9	–
Midshaft anteroposterior diameter[d]	(17.4)	–	–
Midshaft mediolateral diameter[d]	(17.5)	–	–
Midshaft circumference[d]	(53)	–	–

[a] maximum anteroposterior diameter from the dorsal surface of the bone to the anterior tip of the coronoid process (McHenry *et al.*, 1976).
[b] maximum and minimum diameters of the articular facet for the radial head.
[c] taken at the level of the distal border of the ulnar tuberosity (McHenry *et al.*, 1976).
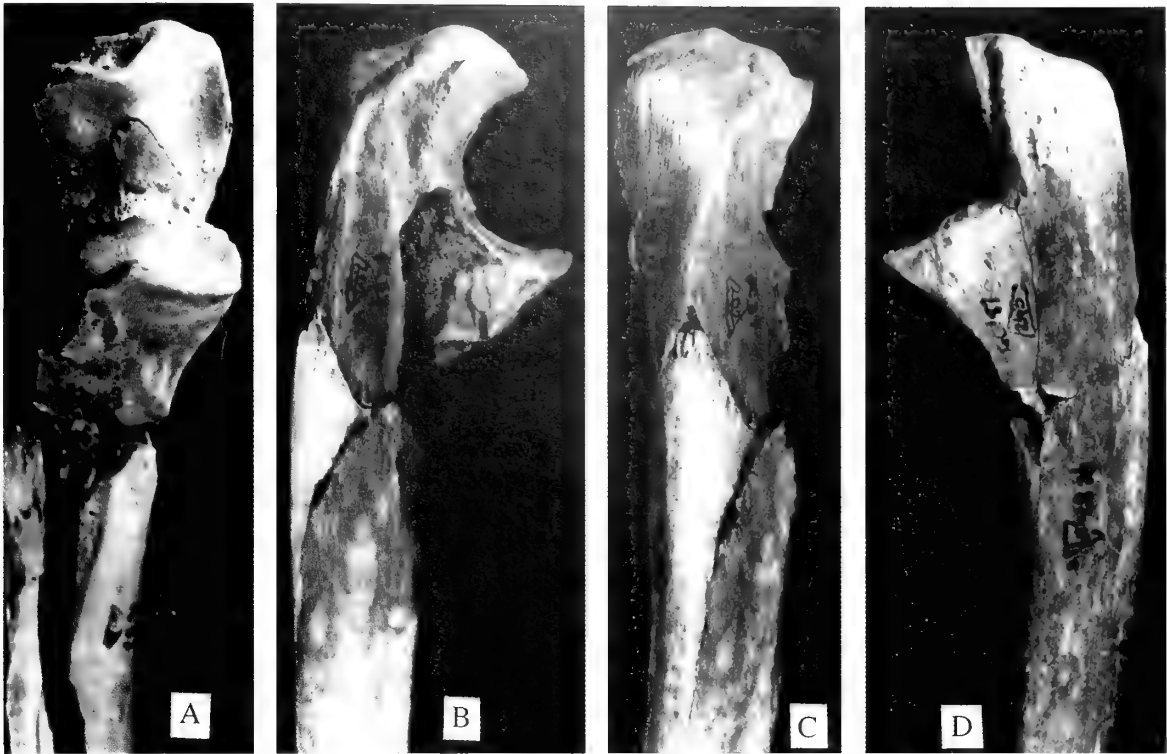[d] midshaft location estimated.

Fig. 14 Right ulna, M.54066, proximal, natural size. **14A,** anterior; **14B,** lateral; **14C,** posterior; **14D,** medial.
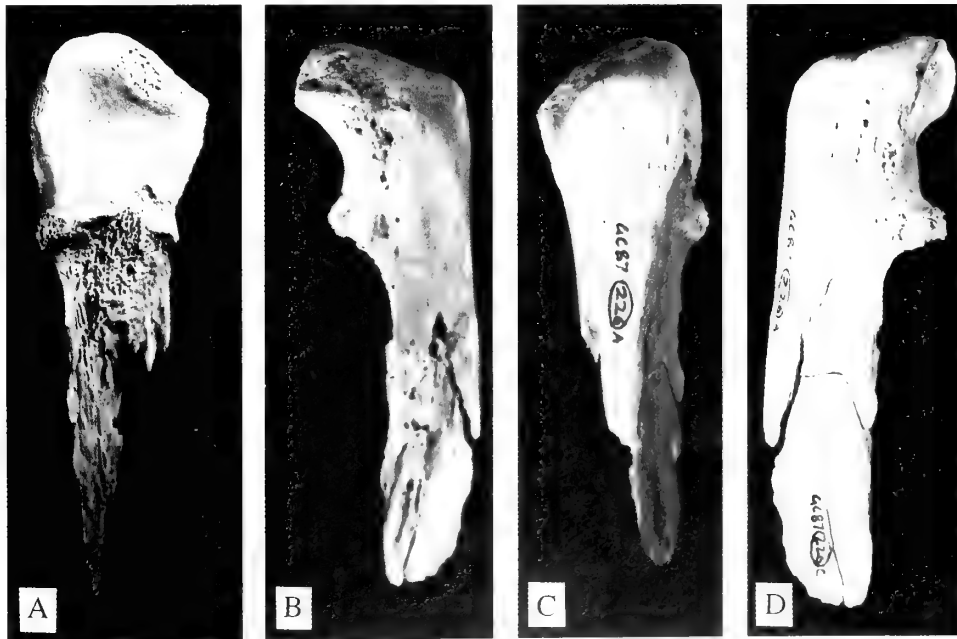

Fig. 15 Left proximal ulna, M.54067, natural size. **15A,** anterior; **15B,** lateral; **15C,** posterior; **15D,** medial.

olecranon process is preserved on the volar surface, and the entire coronoid process and volar surface of the shaft is missing distally. More bone is preserved on the dorsal surface, which is broken distally about half way along the *M. anconeus* insertion. There is some erosion to the volar-most tip of the olecranon process.

The *M. anconeus* insertion area is smooth, and the *M. triceps brachii* insertion is also non-rugose. A small portion of the proximal end of the *M. supinator* crest can be seen near the broken volar
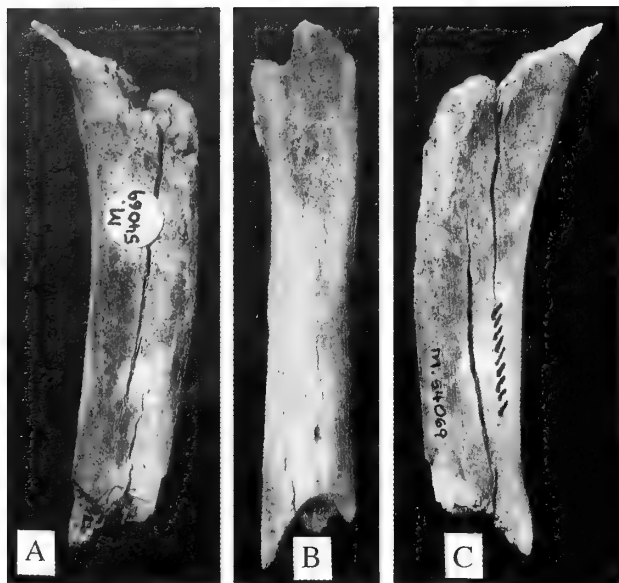
Fig. 16 Right ulna, M.54069, natural size. **16A,** medial; **16B,** anterior; **16C,** lateral.

surface, and this crest is only mildly rugose. There is only a slight crest evident separating the olecranon and coronoid articular surfaces in the trochlear notch.

M.54068 (GC 87 209) (not figured)
Left
This is a 121.2mm long (by 15.0mm wide) fragment of left ulnar diaphysis. The fragment preserves only the dorsal surface (and part of the dorsolateral surface up to the inferior edge of the interosseous crest). The specimen is preserved from the region of the distal *M. anconeus* insertion (with cutmarks at the very distal end of the insertion area) proximally to around midshaft distally. Cutmarks can also be seen on the dorsal surface at the very distal end of the fragment.

The morphology of this specimen compares favourably with the right ulna M.54066 (see above), and M.54068 may represent its antimere and the distal portion of the left proximal ulnar fragment M.54067 (see above).

M.54069 (GC 420.1: Level 12, 1950–51 excavations) (Fig. 16)
Right
This is a fragment of a right ulnar diaphysis, from just proximal of the *M. brachialis* scar to just distal of the proximal end of the interosseous crest. The total length of the fragment is 70mm. The bone is small and gracile and possibly represents a subadult. The bone surface is weathered or calcined. Cutmarks are visible on the superomedial margin of the diaphysis near the distal break.

The *M. brachialis* scar is not rugose but the muscle attachment area can be clearly discerned. What appears to be the distal part of a small *M. supinator* crest is visible on the lateral side. The *M. anconeus* also appears to be only mildly rugose, but there is damage to the inferior-proximal surface making evaluation of the muscle marking morphology difficult.

M.54070 (GC 87 118 B) (not figured)
Left
This is a 47.8mm by 9.1mm diaphyseal fragment of the anteromedial shaft of a distal left ulna. The fragment preserves the distal-most two centimeters of the *M. pronator quadratus* crest (which is distinct but not markedly large) and the metaphyseal region just proximal of the head.

Morphology

The Gough's Cave Creswellian ulnar assemblage represents a minimum of two individuals, one relatively large (male?) and one smaller and more gracile (perhaps female or juvenile). The right ulnar fragment M.54066 and the left ulnar fragments M.54067 and M.54068 are sufficiently similar in size and morphology to suggest that they derive from the same individual. Especially noteworthy is the observation that both bones have generally non-rugose muscle scars, yet both show a more pronounced (although still moderate) development of the attachment area of *M. supinator*. While none of these three specimens exhibit marked muscular rugosity, the external dimensions of the bones tend to be comparable to or greater than the mean values obtained for the late Upper Palaeolithic male sample (Table 9), supporting the suggestion that these remains derive from a male. In terms of mid-proximal shaft cross-sectional strength measures (Table 10), the right ulna M.54066 falls above the values obtained for the male specimen Gough's Cave 1.

A smaller individual is represented by the right ulnar fragment M.54069. This specimen has proximal shaft dimensions that are small even relative to Upper Palaeolithic females (Table 9).

Table 9 Comparative ulnar osteometrics (mean, SD, n).

Right ulnae	M.54066	M.54069	U.P.♂	U.P.♀
Olecranon length	20.8	–	16.8, 3.0, 11	16.7, 2.0, 4
Olecranon height	24.4	–	26.7, 1.8, 11	23.8, 1.4, 4
Olecranon breadth	26.3	–	25.7, 1.4, 10	24.1, 0.7, 3
Trochlear notch chord	23.7	–	26.8, 4.0, 8	22.7, 2.7, 3
Coronoid height	37.1	–	37.3, 1.8, 8	33.0, 1.1, 5
Radial facet maximum diam.	(>15)	–	16.4, 1.9, 7	16.4, –, 2
Radial facet minimum diam.	[9.5]	–	11.4, 0.7, 7	11.2, –, 2
Proximal AP diameter	18.1	14.7	15.1, 1.5, 8	15.9, 2.5, 3
Proximal transverse diam.	18.9	11.3	15.8, 1.5, 8	14.4, 0.5, 3
Proximal circumference	–	45	49.6, 3.2, 8	46.3, 2.5, 3
Left ulna	M.54067		U.P.♂	U.P.♀
Olecranon length	18.2		16.9, 2.9, 11	15.9, 2.1, 3
Olecranon height	(25)		25.0, 1.8, 11	21.4, 1.1, 3
Olecranon breadth	25.2		24.7, 2.0, 10	23.6, –, 1

All measurements are in millimeters and are defined in Table 8.

Table 10 Comparative right ulnar mid-proximal cross sectional geometric properties.

	M.5406	Gough's Cave 1
Total area (TA) (mm^2)	208.7	143.0
Cortical area (CA) (mm^2)	176.0	131.3
Medullary area (MA) (mm^2)	32.7	11.7
AP 2nd moment of area (I_x) (mm^4)	3641.9	1632.5
ML 2nd moment of area (I_y) (mm^4)	3529.8	1920.1
Max. 2nd moment of area (I_{max}) (mm^4)	4048.3	2096.7
Min. 2nd moment of area (I_{min}) (mm^4)	3123.3	1455.9
Polar 2nd moment of area (J) (mm^4)	7171.7	3552.6
Percent cortical area (%CA)	84.3	91.8
I_x/I_y	1.03	0.85
I_{max}/I_{min}	1.30	1.44

Fig. 17 Right radius, M.54071, natural size. **17A,** medial; **17B,** anterior; **17C,** lateral (note engraving).

RADIAL REMAINS

M.54071 (GC 87 60 A, 65, 74, 100, & 108 G) (Figs 17, 18)
Right

Five fragments conjoin to make up a portion of the mid-to-distal diaphysis of a right radius (Fig. 17). The dorsolateral surface of the diaphysis is engraved with a series of carat-shaped marks (Fig. 18: see also Andrews & Fernandez-Jalvo, this series of papers). The total length of the fragment is 156.1mm. Only a portion of the distal dorsal shaft and the lateral shaft (from midshaft region to the distal metaphyseal region) are preserved. On the distal-most part of the dorsal surface, several small nutrient foramina can be seen, as well as the beginning of the crest for *M. brachioradialis*. The fragment is broken medially before the dorsal (Lister's) tubercle. Proximally, a portion of the *M. pronator teres* scar can be seen on the superolateral shaft.

If the *M. pronator teres* scar is used as a rough indicator of midshaft, this specimen can be aligned with the estimated midshaft of the M.54066 ulna. Observation of the specimens in this alignment reveals that the two bones may well have belonged to the same individual. Furthermore, the overall size and morphology of this specimen matches well that of the left radial fragment M.54074/ M.54075 (below), and likely represents its antimere.

M.54072 (GC 87 142) (Fig. 19)
Left

This specimen preserves 26.2mm of the anterior portion of the head and neck and the proximal margin of the radial tuberosity of a left radius. The articular rim is eroded on the medioposterior side of the head and the bone is missing from just posterior of the central depression of the head.

The anterior rim of the articular surface of the head does not dip distally towards the radial tuberosity as it does in most radii, but the same morphology can occasionally be seen in recent human radii (personal observation). The subperiosteal bone of the neck slopes mildly anteriorly and blends with the articular rim, such that there is not a steep drop-off from the articular to the non-articular surface as seen in most radii, but again a similar morphology can occasionally be found in recent human radii (personal observation).

The head is moderately large (mediolateral diameter of the head = 23.4mm; proximodistal length of the proximal ulnar facet = 6.2mm) and the neck appears wide (neck mediolateral diameter = 15.9mm). The proximal margin of the radial tuberosity appears to be relatively proximally positioned (*i.e.* is not very far down the shaft), suggesting a short head-neck length in this individual. This specimen may represent the antimere of M.54073 (see below).

M.54073 (GC 87 235) (not figured)
Right?

This is a fragment of a proximal radius including a portion of the proximal (capitular) articular surface, the anterior articular rim (preserving the 'dip' in the anterior articular surface) and a sliver of the neck down to the beginning of the radial tuberosity. The total fragment length is 24.2mm. When seen in anterior view, the superior articular surface seems to rise slightly to the right, suggesting that this represents a right side radius.

In addition to a general congruence in size, two aspects of morphology are similar to that seen in M.54072 (above). First, the distance from the articular surface (on the anterior aspect) to the beginning of the *M. biceps brachii* scar is the same as that of M.54072. Second, the distal margin of the anterior articular surface slopes onto the neck subperiosteal surface, with no sharp drop. This specimen most likely represents the antimere of M.54072.
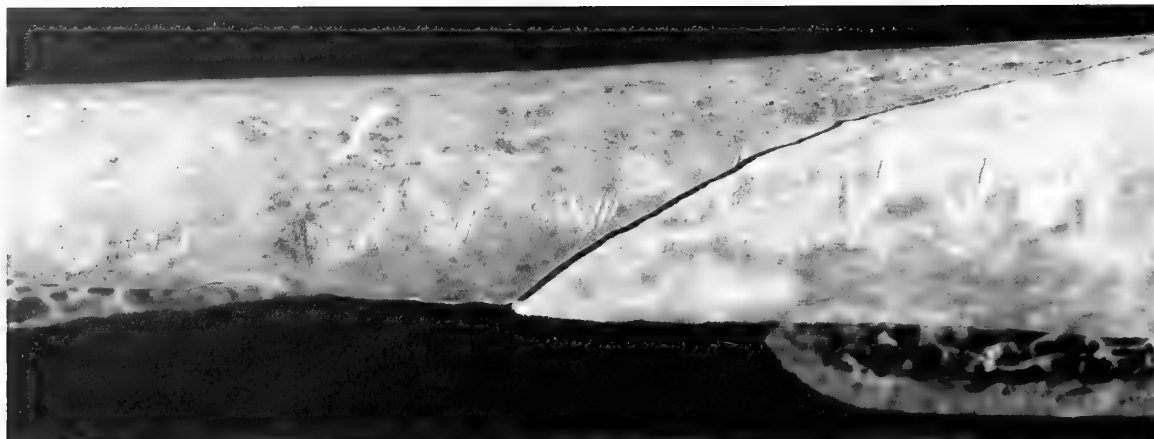
Fig. 18   Right radius, M.54071, detail of engravings. 3x natural size.

Fig. 19   Left proximal radius, M.54072, anterior view. Natural size.

M.54074, M.54075 (GC 87 65, 100, 108 E, 118 A, 123 C & 152) (Fig. 20)
Left
Six fragments conjoin to form a portion of the diaphysis of a left radius. The diaphysis preserves only a small portion of the volar surface along the medial side from just inferior of the radial tuberosity to distal of midshaft, as well as some volar surface in the distal metaphyseal region. Virtually the entire medial surface, preserving the interosseous crest, is present from just distal of the radial tuberosity to the distal metaphysis. Dorsally, only the medial side of the proximal shaft is preserved, but the dorsal surface is largely complete from the region of midshaft to the distal metaphysis. None of the distal articular surfaces are preserved, but the medial-most dorsal (Lister's) tubercle is preserved. The lateral surface of the shaft is present only in the region of midshaft, where it preserves a portion of the *M. pronator teres* insertion, which is well defined and rugose.

In size and morphology this specimen matches M.54071 (above), and probably represents its antimere.

M.54076 (GC 1949–51 Level 13) (not figured)
Right
This specimen preserves 110.3mm of a right radial diaphysis. The fragment preserves a portion of the interosseus crest and the distal end of the anterior ridge (the ridge that extends distally from the radial tuberosity and gives rise to the radial head of *M. flexor digitorum superficialis*). The proximal portion of the shaft preserves some of the lateral and dorsal surfaces, while distally only the medial and dorsal surfaces are preserved.

Morphology

Little can be said about the comparative morphology of the Gough's Cave radii, since muscle scars and articular surfaces are poorly represented. The five Creswellian radial remains described above may all derive from a single individual. This individual was probably male (on the basis of size and the moderate rugosity of the *M. pronator teres* scar in M.54074/M.54075), adult (judging from the state of fusion of the preserved portion of the distal epiphysis in M.54071) and may be the same individual represented by the fragmentary ulna M.54066.

MANUAL REMAINS

M.54077 (GC 87 221(?)) (not figured)
This specimen preserves the head of a metacarpal, probably from the fourth or fifth ray, side indeterminate. The distal epiphysis is fully fused.

M.54078 (GC 87 221 D) (not figured)
Right
This is a 56.0mm long fragment of the diaphysis of what is most likely a right second metacarpal. The specimen preserves a small bit of articular surface proximally that likely represents the third metacarpal articular facet, and an epiphyseal plate distally (with the head unfused). The metacarpal heads usually unite with the shafts in the

Table 11   Dimensions (mm) of manual phalanx fragment M.54079.

Midshaft height[a]	7.0
Midshaft breadth[a]	(11.8)
Midshaft circumference[a]	(33)
Distal height[b]	8.0
Distal maximum breadth[c]	11.7
Distal articular height[d]	11.2

[a] Maximum dorsovolar and radioulnar diameters and circumference at midshaft (midshaft location estimated). In the case of breadth and circumference, the proximodistal crack in the palmar surface of the bone has slightly inflated the measurements.
[b] Dorsovolar diameter of the head.
[c] Maximum radioulnar diameter of the head.
[d] Maximum radioulnar diameter of the articular facet of the head.

Fig. 20 Left radius, M.54074 and M.54075, natural size. **20A**, anterior; **20B**, medial; **20C**, posterior; **20D**, lateral.

fifteenth to sixteenth year in females, or in the eighteenth to nineteenth year in males (Williams & Warwick, 1980).

M.54079 (GC 87 175 A) (Fig. 21)

This specimen is a proximal phalanx lacking its proximal end, with a total length of 37.7mm (Fig. 21). The side is indeterminate. The proximal end is damaged and the epiphysis is missing. The damage is close to the epiphyseal line (the nutrient foramina are visible) but not enough of the region survives to know whether or not the

epiphysis was fused. There is a large crack running proximodistally along the palmar surface of the diaphysis, as well as some damage to one side of the shaft at the proximal end. The transverse diameter of the shaft expands gradually from distal to proximal, and in this aspect the specimen most closely resembles that of a proximal phalanx from the third or fourth ray. The crests for attachment of the fibrous sheaths for *Mm. flexor digitorum profundus* and *f. d. superficialis* are well marked and prominent on this specimen.
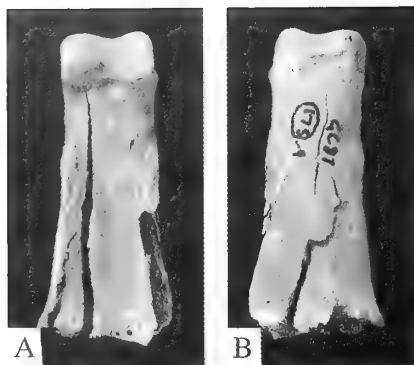
Fig. 21   Proximal phalanx, M.54079, natural size. **21A**, palmar; **21B**, dorsal.

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Gough's Cave 1 (Somerset, England): a study of the hand bones

ERIK TRINKAUS

Department of Anthropology, Campus Box 1114, Washington University, St. Louis, MO 63130, USA, and U.M.R. 5809 du C.N.R.S., Laboratoire d'Anthropologie, Université de Bordeaux I, 33405 Talence, France

SYNOPSIS. The Gough's Cave 1 hand remains preserve five metacarpals and two proximal phalanges. Average metacarpal to arm length is similar to that of Holocene and Recent humans. Proximal phalanx length relative to metacarpal length is moderately short. Also of note is the general gracility of the hand, and the angular deviations of the metacarpo-phalangeal and proximal interphalangeal articulations away from a midline through the fourth ray.

INVENTORY

The hands of Gough's Cave 1 are represented by five metacarpals and two proximal phalanges (Fig.1). From the right hand are metacarpals 2 to 5, which are complete with minimal dorsal, radial and distal abrasion to the metacarpal 3. The left hand retains the complete metacarpal 4 plus the complete proximal phalanges 2 and 5; digit identification of the proximal phalanges is based their base morphologies (radial first dorsal interosseus tubercle on proximal phalanx 2 and ulnar *M. abductor digiti minimi* facet on proximal phalanx 5) and radial versus ulnar deviations of their heads. The osteometric measurements for these elements are in Tables 1 and 2.

In addition, midshaft cross-sectional geometric parameters (cross-sectional areas and second moments of area) are provided, even though comparative data are not currently available. The values were calculated from external diameters and cortical thicknesses determined from radiographs and then corrected for parallax enlargement, using standard ellipse formulae (Runestad *et al.*, 1993).

OVERALL HAND PROPORTIONS

Assessment of the overall proportions of the Gough's Cave 1 hand remains is limited by the dearth of comparative metrics for associated hand and arms remains, as well as the limited elements preserved for Gough's Cave 1.

It is nonetheless possible to compare the articular length of the metacarpal 3 to the summed humeral and radial articular lengths (averaging the right and left humeral articular lengths). The resultant ratio provides an index of 11.6. This value is close to the means of recent European and Amerindian samples [11.9 ± 0.5, N = 11; 11.7 ± 0.5, N = 19 (Trinkaus, 1983)]. Similarly, a ratio using the metacarpal 3 maximum length provides an index of 12.4 for Gough's Cave 1, which matches the highest of such indices for the Mesolithic remains from Arene Candide [AC 2: 11.6; AC 5: 12.4 (Paoli *et al.*, 1980)], Culoz 2 [12.0 (Genet-Varcin *et al.*, 1963)], and Le Peyrat 5 [11.9 (Patte, 1968)]. As with other Primates (Schultz, 1930) and members of the genus *Homo* (Trinkaus, 1983), the relative hand length of Gough's Cave 1 indicated by its metacarpal 3 length is similar across these European Holocene samples.

Proportions within the hand can be assessed by comparing proximal phalangeal lengths to metacarpal lengths for digits 2 and 5, even though this assumes near bilateral symmetry in metacarpal and phalangeal lengths given that Gough's Cave 1 preserves those

metacarpals on the right side and the phalanges on the left side.

The ratio of proximal phalanx 2 articular length to metacarpal 2 articular length gives an index of 56.7 for Gough's Cave 1, a value which is low but not exceptionally so compared to a recent British sample [59.8 ± 1.7, N = 38 (Musgrave, 1970)]. The same index for the fifth digit gives a value of 58.0 for Gough's Cave 1, which is similarly relatively low compared to a recent British sample (61.2 ± 2.6, N = 38). Alternatively, using maximum lengths, the Gough's Cave 1 phalanges and metacarpals can be compared to values for the Mesolithic Arene Candide 2 and 5 specimens (Paoli *et al.*, 1980). The resultant Gough's Cave 1 second and fifth ray indices are 58.2 and 62.0, both of which fall between the values for the Arene Candide specimens of 60.4 and 57.7 respectively for the second digit and 63.3 and 59.4 respectively for the fifth digit.

Consequently, the hand remains from Gough's Cave 1 exhibit metacarpal to arm length proportions similar to those of other European Holocene samples but, along with at least two other European Mesolithic specimens, possess moderately short proximal manual phalanges compared to a recent European sample.

METACARPAL MORPHOLOGY

The Gough's Cave 1 metacarpals are relatively large but appear variably gracile in their external surface morphology.

Most of the ridges for the dorsal interosseus muscles on the diaphyses are evident but do little more than provide an angulation between the dorsal plane of the diaphysis and the radial and ulnar surfaces. However, the radial dorsal ridge on the right metacarpal 2 for the first dorsal interosseus muscle is slightly more pronounced, forming a raised ridge from midshaft proximally to the radial side of the dorsal proximal epiphysis. The metacarpal 2 dorso-radial ridge is accompanied by a distinct concavity to the radial side of the metacarpal 2 diaphysis, which is bordered palmarly by a sharp crest extending from the radial head to the radial base but curving distinctly ulnarly near midshaft. A similar but less pronounced crest is evident on the distal half of the palmar metacarpal 3 diaphysis, and there is only a suggestion of similar relief on the palmar metacarpal 4 diaphysis.

There is no trace of the insertion of the *M. opponens digiti minimi* on the right metacarpal 5, and the ulnar tubercle on the base of the metacarpal 5 for the *M. extensor carpi ulnaris* tendon projects obliquely distally from the carpal articular surface and only moderately beyond the ulnar margin of that carpal articular surface. The last is reflected in the small difference (2.5mm) between the metacarpal 5 proximal maximum and articular breadths.
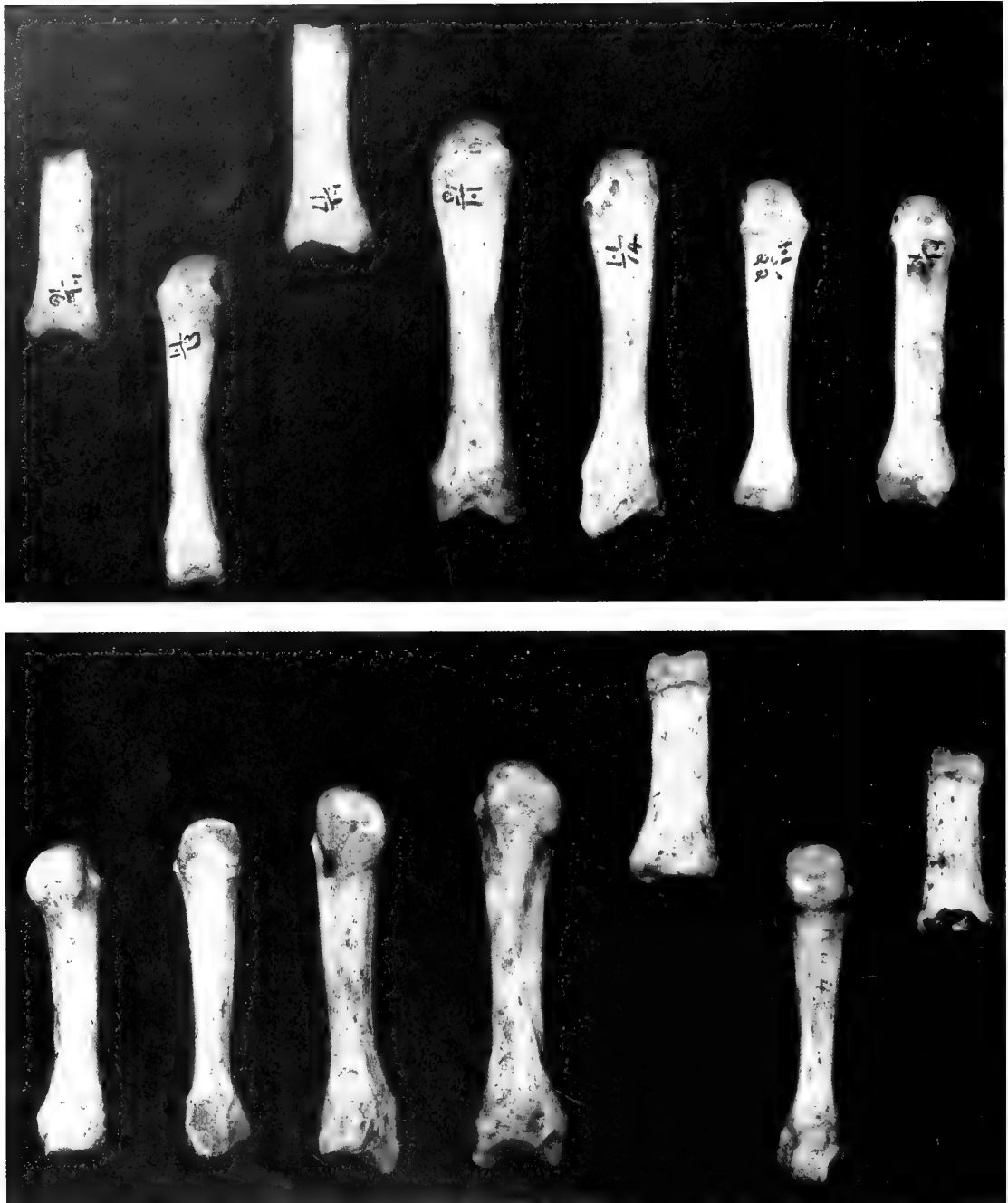
Fig. 1 Dorsal (above) and palmar (below) views of the Gough's Cave 1 metacarpals and proximal manual phalanges; × 0.9.

This surface gracility is reflected in a metacarpal 3 robusticity index [midshaft height * breadth)$^{1/2}$ / articular length] of 13.1 for Gough's Cave 1. This value is below that of the Le Peyrat 5 right metacarpal 3 [15.0 (Patte, 1968)] and the mean of a modern British sample [14.4 ± 1.2, N = 38 (Musgrave, 1970)].

The metacarpal 2 base has a large concave surface for the trapezoid bone, accompanied by facets for the trapezium and capitate at right angles to each other and close to 45° from the diaphyseal axis. The angle of 50 for the capitate facet is close to the mean of a recent Euroamerican sample [56.0° ± 9.3°, N = 53 (Niewoehner et al., 1997)]. In conjunction with this oblique orientation of the Gough's Cave 1 metacarpal 2 / capitate articulation, Gough's Cave 1 possesses a large and projecting metacarpal 3 styloid process. The index of styloid projection (styloid projection vs. metacarpal 3 articular length) for Gough's Cave 1 is 6.6. This value is close to the mean for a recent Euroamerican sample of 7.4 [± 1.7, N = 33 (Niewoehner et al., 1997)] and below that for the Le Peyrat 5 right metacarpal 3 [8.6 (Patte, 1968)]. The metacarpal 5 base combines

Table 1 Osteometrics of the Gough's Cave 1 metacarpals. Measurements in millimeters or degrees except for cross-sectional areas (mm²) and second moments of area (mm⁴).

Digit & side Catalog number	2 right 1.1/15	3 right 1.1/14	4 right 1.1/13	4 left 1.1/22	5 right 1.1/12
Maximum length	71.0	68.3	58.9	59.3	55.0
Articular length[1]	67.5	64.1	57.6	57.9	54.3
Midshaft height	8.6	8.3	7.2	6.9	6.9
Midshaft breadth	9.1	8.5	6.6	6.7	8.3
Midshaft circumference	27.5	26.5	22.5	23.0	24.0
Midshaft total area	61.4	55.4	37.3	36.3	45.0
Midshaft cortical area	49.8	43.7	28.8	29.1	31.7
Midshaft medullary area	11.7	11.7	8.5	7.2	13.3
Midshaft AP 2nd moment of area	273.3	228.3	115.4	103.7	123.4
Midshaft ML 2nd moment of area	307.0	238.3	95.6	97.9	174.7
Midshaft polar moment of area	580.3	466.6	211.0	201.6	298.1
Proximal maximum height	17.3	16.7	11.5	11.4	11.1
Proximal maximum breadth	15.3	13.7	11.4	10.7	13.6
Proximal articular height	15.9	15.3	10.7	10.3	9.0
Proximal articular breadth	11.1	11.8	10.6	9.4	10.1
Distal height	13.6	13.4	11.6	11.3	11.5
Distal maximum breadth	14.8	13.6	12.1	12.1	11.6
Distal articular breadth	13.3	12.9	10.8	11.2	11.0
Trapezium articular breadth[2]	4.3				
Trapezium angle[3]	40°				
Capitate articular breadth[4]	2.7				
Capitate angle[5]	50°				
Styloid projection[6]		4.2			
Hamate subtense[7]	0.8				
MC 2 articular breadth[8]		6.2			
MC 3 articular breadth	6.3		7.2	6.4	
MC 4 articular breadth		5.2			3.9
MC 5 articular breadth			5.3	5.0	

[1] Direct distance between the middle of the primary carpal articular facet and the most distal point on the head; [2] Disto-radial to proximo-ulnar diameter of the facet for the trapezium on the metacarpal 2; [3] Angle, in the coronal plane of the metacarpal, between the plane of the trapezium facet and the diaphyseal axis of the metacarpal; [4] Maximum proximo-radial to disto-ulnar breadth of the facet for the capitate on the metacarpal 2; [5] Angle, in the coronal plane of the metacarpal, between the plane of the dorso-palmar middle of the capitate facet and the diaphyseal axis of the metacarpal 2; [6] Proximal projection of styloid process from the capitate surface (= Max.Len. – Art.Len.); [7] Subtense from the articular breadth of the proximal metacarpal 5 facet to the furthest point on the middle of the articular surface. A positive subtense indicates a radio-ulnarly concave facet; [8] 'MC # articular breadth' indicates the predominantly proximo-distal diameter of the facet for the indicated adjacent metacarpal base.

Table 2 Osteometrics of the Gough's Cave 1 manual proximal phalanges. Measurements in millimeters or degrees except for cross-sectional areas (mm²) and second moments of area (mm⁴).

Digit & side Catalogue number	2 left 1.1/17	5 left 1.1/16
Maximum length	41.3	34.1
Articular length[1]	38.3	31.5
Midshaft height	6.2	5.8
Midshaft breadth	10.2	9.6
Midshaft circumference	27.0	26.0
Midshaft total area	49.6	43.7
Midshaft cortical area	43.1	37.1
Midshaft medullary area	6.6	6.6
Midshaft AP 2nd moment of area	118.3	90.5
Midshaft ML 2nd moment of area	310.4	243.0
Midshaft polar moment of area	428.7	333.5
Proximal maximum height	11.5	10.7
Proximal maximum breadth	16.0	14.3
Proximal articular height	9.5	8.5
Proximal articular breadth	11.8	10.9
Distal height	8.2	7.1
Distal maximum breadth	11.5	10.2
Distal articular breadth	10.7	9.6
Horizontal angle[2]	–4°	13°
Vertical angle[3]	1°	7°

[1] Miminum distance from the deepest point in the proximal base to the middle of the distal trochlea; [2] Angle, in the coronal plane of the bone, between the tangents to the proximal and distal articulations. A positive angle indicates a relative ulnar deviation of the distal articulation; [3] Angle, in the parasagittal plane of the bone, between the tangent to the proximal articulation and the diaphyseal axis. A positive angle indicates a dorsal deviation of the proximal articular plane.

its small ulnar tubercle with a hamate surface with a distinct radio-ulnar concavity.

The heads of the metacarpals are of note only for their degrees of radial or ulnar deviation. Only the metacarpal 4 head is in line with its diaphysis. The metacarpal 5 head is strongly ulnarly directed, whereas the metacarpal 3 and especially metacarpal 2 heads are radially shifted.

PROXIMAL MANUAL PHALANGEAL MORPHOLOGY

The two preserved proximal manual phalanges, like the meta-carpals, have weak to moderate muscle markings. There are clear ridges for the flexor tendon sheaths, but they project little from the palmar margins of the diaphyses. There are clear, oblique facets for the first dorsal interosseus muscle on the radial base of the proximal phalanx 2 and for *M. abductor digiti minimi* on the ulnar base of the proximal phalanx 5, but neither one is exceptional in its development.

Both bases are slightly dorsally oriented. At the same time, the head of the proximal phalanx 2 is moderately deviated radially and the head of the proximal phalanx 5 is strongly ulnarly deviated. Both of these angles combine with the respective radial and ulnar deviations of the associated metacarpals (even if those are evident only on the contralateral digits), to accentuate an apparent spread of the fingers, at least under conditions of habitual loading.

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A revision of the English Wealden Flora, III: Czekanowskiales, Ginkgoales & allied Coniferales

JOAN WATSON & SUSANNAH J. LYDON
Department of Earth Science, Williamson Building, The University, Manchester M13 9PL
NICOLA A. HARRISON
Atos Origin, Wilton Centre Annexe, PO Box 54, Wilton, Middlesbrough, TS90 8JA, UK

CONTENTS

SYNOPSIS. Eleven gymnosperm leaf species are identified and described from the English Wealden flora, attributed to the orders Czekanowskiales, Ginkgoales and needle-leaved Coniferales. All occur as fragments in the 'plant debris beds' which are common throughout the Wealden succession in East Sussex, Dorset and the Isle of Wight. Two new species assigned to the Czekanowskiales are placed in the genera *Czekanowskia* Heer and *Phoenicopsis* Heer; three new species assigned to the Ginkgoales are placed in the form-genus *Ginkgoites* Seward; an ovule containing monosulcate pollen grains, associated with one of the *Ginkgoites* leaves is described and illustrated. Needle-leaved conifers of uncertain family attribution comprise two species assigned to the genus *Pseudotorellia* Florin, one species to *Sciadopityoides* Sveshnikova. The shoot species *Sulcatocladus robustus* Watson & Harrison is known to be attributable to the leaf species *Pseudotorellia linkii* (Römer); a second species of *Sulcatocladus* Watson & Harrison is attributed to the new species of *Sciadopityoides*. A leaf species with stomata in two grooves is referred to the form-genus *Torreyites* Seward and tentatively to the family Taxaceae. The Czekanowskiales are recorded from the Lower Cretaceous of western Europe for the first time and the palaeoecological implications of these additions to the English Wealden flora are discussed.

INTRODUCTION

Since the early work of Watson (1969) on a revision of the English Wealden flora, previously studied by Seward (1894, 1895, 1913), a large amount of new material has become available from plant debris beds which occur widely throughout the succession. This dispersed, fragmentary material shows exceptional cuticular preservation and has been extensively studied, particularly by scanning electron microscopy, to yield a considerable volume of new information which greatly adds to our knowledge of the flora and necessitates significant changes to the floral list (Watson & Alvin 1996). This material is by nature usually comminuted and the leaf fragments attributed to the orders Czekanowskiales and Ginkgoales have been placed within these higher taxa largely on the basis of cuticular characters, though gross morphological features such as segment width and evidence of a petiole are available from some specimens. Five new czekanowskialean and ginkgoalean species are presented together with consideration of changes made since the previous assessment of the flora which included the Ginkgoales (Watson 1969). The Ginkgoales were then represented only by the single species *Pseudotorellia heterophylla* Watson, which has since been synonymized and recombined as *Pseudotorellia linkii* (Römer) Watson & Harrison (1998). The studies of Hall (1987) and Watson & Harrison (1998) indicate that the affinities of this species, together with other needle-leaved forms of uncertain systematic position, are more likely to lie within the Coniferales. In the meantime four of the five species described here had been added to the flora piecemeal (Oldham 1976; Hall 1987; Watson & Alvin 1996), though none of them has been named until now. Recent stratigraphic work by Lydon (in progress) led to the discovery of the *Czekanowskia* species described here and also necessitated a reconsideration of ginkgoalean leaf genera by Watson, Lydon & Harrison (1999). Only now have the appropriate generic attributions become clear to us, with one species of *Czekanowskia*, one species of *Phoenicopsis* and three species of *Ginkgoites* replacing the species indicated on the floral list by Watson & Alvin (1996). It should be emphasised at this point that the recognition of *Czekanowskia* and *Phoenicopsis* in the English Wealden represents the only known occurrence of the Czekanowskiales in a Lower Cretaceous flora from western Europe. All other recorded occurrences are much further east and most of them further north (Samylina & Kiritchkova 1993), a point which Watson & Alvin (1996: 20) failed to indicate.

All the specimens figured in this paper, including those from the Wealden of Germany, are in the collections of The Natural History Museum, London (NHM – formerly the British Museum (Natural History)), and have numbers prefixed V.

GEOLOGICAL OCCURRENCE

Of the twelve species described here only *Pseudotorellia linkii* is represented by hand specimen material in the old Wealden collections which were accumulated in the late nineteenth and early twentieth centuries and are now housed in various museums (Seward 1894, 1895; Watson 1969; Watson & Sincock 1992). All the other species have been isolated from coaly lenses and partings which occur throughout the English Wealden succession and contain compacted plant fragments often with very little interstitial matrix. The Wealden 'lignite beds' described in the older literature (White 1921; Arkell 1947) are the thickest and most extensive examples of the deposits in question with logs and twigs embedded in compacted plant remains. However, thickness and extent are no guarantee of floral diversity, sometimes the reverse, and tiny lenses which can be collected in their entirety with a sharp knife can yield an impressive mixture of species.

Oldham (1976), in producing the first large-scale study of these beds, introduced the more accurate term 'plant debris bed' for these accumulations of plant material. These beds are present in both sub-basins of the Wealden basin complex: those of the Weald Basin are best developed in the Ashdown Beds Formation, which crops out along the coast at Hastings and Galley Hill in East Sussex; those of the Wessex Basin occur throughout the Wessex Formation, cropping out at Worbarrow Bay, Mupe Bay, Lulworth Cove and Swanage in Dorset, and Sandown and the south west coast on the Isle of Wight. The plant debris beds are thought to be accumulations of plant debris flushed off nearby highlands by heavy rainfall and deposited in depressions on flood plains (Stewart 1981; Allen 1998). Some may have been produced by local storm events and resulting flash floods (Insole & Hutt 1994). They are particularly valuable in yielding exquisitely preserved cuticular material which is mostly from foliage, although some relates to rachises and stems, and some to reproductive structures such as male cones and female cone scales. The plant debris may show lesser or greater levels of pyritization and fusain content. Oldham (1976) considered the beds to be composed entirely of plant material except for the inorganic matrix present, but other workers have shown the beds to be important sources of animal, particularly dinosaur, remains (Freeman 1975; Stewart 1981; Radley 1994; Insole & Hutt, 1994). Of particular interest in this regard is locality L11 of Stewart (1978), the 'Grange Chine Black Band' of the Wessex Formation, at Grange Chine on the South West coast of the Isle of Wight. This locality has produced many vertebrate remains over the last 150 years, including fragments of turtle carapace, crocodile teeth, fragments of jaw and scales of *Lepidotes* and, particularly, remains of dinosaurs. These tend to be worn vertebrae and scraps of ribs but occasional partial skeletons have been noted, particularly of the ornithopod *Iguanodon*. A recent discovery (1998) is that of a 3–4 m long coelurosaur, new to science, which is currently under investigation (Hutt, pers. comm. 2000). The matrix with plant debris material in which this specimen was found embedded has yielded a new species of *Ginkgoites*, described below.

The presence of amber within these beds, in significant amounts in at least one locality (Nicholas *et al* 1993), is also of relevance to the study of the fossil gymnosperms described here.

METHODS

Laboratory methods used to isolate recognisable plant fragments from the debris bed material are of the simplest. The first aim is to do as little damage to the individual plant parts as possible and to this end it is usual to try disaggregation of the matrix in the following order of harshness: hot water alone; hot water with soft-soap; approximately 5% KOH solution. Very few samples have not yielded to KOH but in such cases Schulze's solution can be resorted to. However, this mixture invariably boils and it is essential to use a large bucket with about one inch of debris material in the bottom.

Following disaggregation the resulting sludge is carefully poured from the bucket through a series of three Endecotts brass sieves; 5–10 mm mesh at the top, 2–3 mm in the middle and 400 μm–1 mm at the bottom, depending upon the sample. The residue is very gently but thoroughly washed via a rubber hose on the cold tap. The gently flowing hose is then used from underneath the sieve to wash the plant material into a smaller container (plastic jug) from which, by settling and decanting, it is transferred into screw-top jars and stored in tap

water with Thymol crystals added. Surprisingly large specimens, such as long thin needles, escape through the middle sieve but these can be retrieved before discarding or storing the contents of the bottom sieve. With a mesh size less than 1 mm it is often laden with sediment and usually far too comminuted and voluminous to contemplate long term storage and study. These fractions have in some cases been dried and searched for megaspores etc. with varying degrees of success.

Searching of the concentrates for plant parts is done under water (with thymol) in petri dishes, with low power stereo microscopes, using very fine paint brushes (10 noughts if possible) or sharpened split bamboo sticks. The sorted leaves, shoots, cones, seeds etc. are stored in water/thymol in small, corked glass tubes. For long term storage the cork can be sealed with paraffin wax. Samples prepared in this way by Watson have been successfully stored without fungal growth since 1964.

SYSTEMATIC CONSIDERATIONS

With the first clearly recognisable members of the orders Ginkgoales and Czekanowskiales appearing in the Triassic, their origins and systematic affinities have been long debated. Mesozoic floras from the base of the Jurassic to the Lower Cretaceous span the zenith of both the Ginkgoales and the Czekanowskiales and by the Middle Cretaceous both orders were in decline with the Czekanowskiales becoming extinct before the end of the Cretaceous (Batten 1984). The Ginkgoales continued, but on entering the Tertiary were restricted to a single leaf-genus and soon to a single species which was forced, by the rapid spread of the vigorous angiosperms, into the less hospitable habitats in the northern latitudes (Tralau 1967, 1968). The onset of the Pleistocene ice-age contracted all floristic zones towards the equator; the higher latitude species being forced to retreat to high altitude habitats. The distribution of *Ginkgo biloba* L., the sole surviving member of the Ginkgoales, was contracted to a high altitude *refugium* in China and it is still debated whether *G. biloba* survived truly in the wild in China or was saved from extinction by cultivation in temple gardens (He *et al.* 1997). In modern times the species has been re-introduced in other parts of the world and shows exceptional resistance to extremes of temperature, infection and pollution (Kim *et al.* 1997).

Early studies on the systematic affinities of the Ginkgoales relied upon evidence from *Ginkgo biloba* which has long been recognised as a gymnosperm from the possession of naked ovules. However, its dense wood and habit of bearing long and short shoots initially prompted its inclusion in the conifers (Smith 1797) and the form of the ovules with a fleshy coat and a collar-like structure at the base which was reminiscent of an aril, led to its attribution to the 'Taxineae' (Richard 1826: 135). The discovery by Hirase (1896) of ciliated antherozoids, prompted Engler & Prantl (1897: 19) to remove *G. biloba* from the Coniferales and to erect a new order, the Ginkgoales, to accommodate both the living species and the Mesozoic leaf-genera *Ginkgoites*, *Baiera*, *Phoenicopsis* and *Czekanowskia*. Following the discovery of distinctly non-ginkgoalean ovuliferous structures in *Czekanowskia* (Harris 1951), Pant (1959) established the order Czekanowskiales to which *Czekanowskia*, *Phoenicopsis* and others were assigned. Despite this, the Ginkgoales (*s.s.*) and the Czekanowskiales have continued to be treated, in the main, as closely related orders.

Most workers (Seward & Gowan 1900; Chamberlain 1935; Arnold 1947, 1948; Florin 1949, 1951; Meyen 1982; Stewart 1983) have agreed that the Ginkgoales (*sensu lato*) evolved, if not from the

Cordaitales, then from the same ancestral stock. Opinion has varied as to whether the ancestral stock was in the pteridosperms or the group which gave rise to them. Chamberlain (1935: 432) entertained the possibility that the Ginkgoales and the Cordaitales had their origins in the Pteridospermales. Palaeobotanical evidence presented by Arnold (1948) rendered the pteridosperm-origin of the Ginkgoales unlikely, with pteridosperms evoked as the ancestors of the cycads and bennettites, all being linked by the possession of manoxylic wood, frond-like leaves and, as proposed later (e.g. Sporne 1965: 30), radially symmetrical (radiospermic) seeds. This was the core of the cycadophyte line (Arnold 1948) which remained distinct from the other main group of gymnosperms, the coniferophytes, as far back as could be traced. The coniferophytes, consisting of the cordaites, conifers, ginkgoes (and taxads), was characterised by pycnoxylic wood, simple leaves and bilaterally symmetrical (platyspermic) seeds, with origins unknown (Arnold 1948). This fundamental concept of two main gymnosperm clades, the Cycadopsida and the Coniferopsida required the assumption of a di- (or even poly-) phyletic origin of seed plants, thus rendering the gymnosperms as a group of plants with a common level of organisation (naked ovules) rather than the natural taxon Gymnospermae. The discovery by Beck (1960) of the Devonian Progymnospermophyta, however, provided a possible common basal stock for the cycadopsids and coniferopsids and led some (e.g. Beck 1976; Rothwell 1981) to postulate a monophyletic origin of the gymnosperms. However, two groups have also been recognised in the progymnosperms, the Archaeopteridales and the Aneurophytales. The possibility that each led independently to the evolution of the seed habit was supported by Beck (1981) who suggested that the Archaeopteridales gave rise to the Coniferopsida including the Ginkgoales and Czekanowskiales and the Aneurophytales to the Cycadopsida. Stewart (1983, text-figs 23.1, 26.1) and Stewart & Rothwell (1993, charts 26.1, 29.1) basically supported Beck (1981) in these derivations, but questioned the traditional assumption of common ancestry for the Ginkgoales and Czekanowskiales. They proposed the retention of the Ginkgoales (*s.s.*) in the Coniferopsida with probable origins in the Cordaitales and the transfer of the Czekanowskiales to the Cycadopsida, possibly having arisen from the Glossopteridales.

Recent progress in the field of molecular phylogenetic analyses, as reviewed by Hasebe (1997), shows that all extant gymnosperms constitute a monophyletic group, and that *Ginkgo* may well have closer affinities to cycads than to conifers, thus challenging the view of Ginkgoales as a member of the clade Coniferopsida.

All the schemes of gymnosperm phylogeny mentioned hitherto envisage a pre-Permian origin of the Ginkgoales (*s.s.*), either from the cordaites in the Carboniferous or directly from the cordaitalean stock, now considered to be the progymnosperms, in the Devonian. However, since no clearly recognisable Ginkgoales are known before the Triassic, this leaves a gap in the scheme which can only be filled by vaguely *Ginkgo*-like Permian leaf-genera of unsubstantiated affinity.

It is also possible to evoke an ancestor for the Czekanowskiales from amongst these Permian genera when only the leaves are considered, although there is no evidence for short shoots such as are characteristic of *Czekanowskia*. However, *Leptostrobus*, the bivalved ovuliferous structure of *Czekanowskia*, shows a remarkable likeness to some pteridosperm fructifications and short shoots covered with bud scales are also known in the pteridosperms (Meyen 1982; text-fig. 2C, D).

From the evidence available it appears that there is a rather more remote relationship between the Czekanowskiales and Ginkgoales than has traditionally been assumed. Nevertheless, it remains con-

venient to study the Ginkgoales and Czekanowskiales together, particularly when dealing with fragmentary leaves and cuticles which can be difficult to distinguish and it would not be prudent to study one without the other.

In tribute to the author Terry Pratchett OBE, all the new fossil plant species diagnosed and described in this paper are named for fictional characters who appear in his series of Discworld novels.

SYSTEMATIC DESCRIPTIONS

GYMNOSPERMAE
Order CZEKANOWSKIALES

Harris (1935) first attributed the cupulate fructification *Leptostrobus* Heer to the leaf genus *Czekanowskia* Heer when studying the Scoresby Sound flora from East Greenland, though at that time the precise nature of the reproductive structure was unclear. When later studying the Middle Jurassic flora of Yorkshire Harris (1951) was able to elucidate the exact structure of the *Leptostrobus* seed capsules and repeated the attribution (see also Harris & Miller 1974). The order Czekanowskiales was subsequently named by Pant (1959) in order to accommodate these associated organs and isolate them from the Ginkgoales. Since then Russian authors (e.g. Krassilov 1972) have confirmed the strong evidence, with the repeated association of *Leptostrobus* not only with *Czekanowskia* leaves but also with those of *Phoenicopsis*. Otherwise there has been little further evidence and other aspects of these plants including the pollen organs remain obscure. Thus the order remains poorly characterised and there is no evidence at present to support a further subdivision of the order into families.

The foliage leaves attributed to the Czekanowskiales are all borne in bundles on short caducous shoots which are covered with small scale leaves. The three main leaf-genera included in the order are *Solenites* Lindley & Hutton, *Czekanowskia* Heer and *Phoenicopsis* Heer. These three genera also share the possession of a single vein entering at the base of the foliage leaf but can easily be distinguished according to gross morphological features. *Czekanowskia* Heer and *Phoenicopsis* Heer which are now known to be represented in the English Wealden flora can be separated thus:

Foliage leaves linear, divided, each with one or two veins.
                                                                    Czekanowskia Heer
Foliage leaves narrowly wedge-shaped with numerous veins.
                                                                    Phoenicopsis Heer

Other czekanowskialean leaf genera are discussed at length by Harris and Miller (1974: 79) and this remains an extremely useful account notwithstanding other treatments by Krassilov (1972) and Samylina & Kiritchkova (1991, 1993). Samylina (1972) established sub-genera within *Phoenicopsis* and later (Samylina & Kiritchkova 1993) within *Czekanowskia*, based on cuticle characters. Despite the difficulties of separating the leaves of the Ginkgoales and Czekanowskiales the cuticle of the latter can be quite distinctive, with characteristic features which include: ordinary epidermal cells arranged in longitudinal files, frequently with oblique or pointed end walls; longitudinal arrangement of haplocheilic stomata; cutinization of inner periclinal walls of isolated cells in the epidermis, particularly the subsidiary cells. This is further discussed and illustrated below.

Genus *CZEKANOWSKIA* Heer

1876   *Czekanowskia* Heer: 65.
1936a   *Czekanowskia* Heer; Florin: 128.
1972   *Czekanowskia* Heer; Krassilov: 72.
1974   *Czekanowskia* Heer; Harris & Miller: 92.
1991   *Czekanowskia* Heer; Samylina & Kiritchkova: 30.
1993   *Czekanowskia* Heer; Samylina & Kiritchkova: 273.

TYPE SPECIES. *Czekanowskia setacea* Heer 1876: 68; pls 5, 6 (cuticle figured by Florin 1936a; text-fig.12).

DIAGNOSIS. [emended by Harris & Miller, 1974: 92] Caducous short shoot covered with persistent scale leaves and bearing bundle of foliage leaves. Foliage leaf, as a whole, wedge-shaped, dividing by dichotomies into number of filiform segments; segments ending in acute apex. Leaf substance thick, probably oval in section. Vein single at leaf base, forking well below lamina dichotomy; apex with single vein. Resin bodies absent.

Cuticle well developed, similar on the two sides, amphistomatic; stomata occurring mainly in more or less short longitudinal files. Stomatal files almost evenly distributed over whole epidermis (including veins and at leaf margins). Stomata longitudinally orientated, haplocheilic, guard cells sunk in pit formed by subsidiary cells, two of which are usually terminal. Pit commonly reduced by rim or papillate pads of subsidiary cells. Encircling cells occasional.

DISCUSSION. Cuticles from the two sides of *Czekanowskia* foliage leaves are not easily designated 'upper' and 'lower' and indeed these terms are less appropriate for leaves which are borne in bundles. The wider leaves of *Phoenicopsis* sometimes exhibit a dorsi-ventral differentiation and the cuticles are then designated 'thicker' and 'thinner', possibly upper and lower respectively. The narrow one- or two-veined leaves of *Czekanowskia* exhibit no such differentiation and the reason for this might be apparent in some Jurassic uncompressed *Czekanowskia* leaves which have been described as round in transverse section by Hill (C.R. Hill, pers. comm. 1987). In such leaves, the description of cuticle from each 'leaf-surface' in the compression fossil, loses its value. Nevertheless, two distinct surfaces can be detected on the grounds of stomatal density. Samylina and Kiritchkova (1991, 1993) have described the leaf cross-section as trapezium-like or rectangular but this is not confirmed in Yorkshire Jurassic material or from the Wealden specimens.

Three subgenera within the genus *Czekanowskia* Heer have been recognised by Samylina & Kiritchkova (1991, 1993). These are: subgenus *Czekanowskia* with amphistomatic leaves, stomata in files; subgenus *Harrisella* with amphistomatic leaves, stomata in bands at least on lower epidermis; subgenus *Vachrameevia* with hypostomatic leaves, stomata in files or bands. Seventy four species of *Czekanowskia*, from more than 160 Mesozoic localities in the Northern Hemisphere, divided between these three subgenera are listed by Samylina & Kiritchkova (1991). All of the Lower Cretaceous occurrences are geographically extremely remote from the Wealden.

Czekanowskia anguae sp. nov.   Figs 1–3

DIAGNOSIS. [based on leaf fragments only] Leaf 1–2 mm wide, more than 6 mm long, tapering to mucronate apex [veins unknown]. Stomata present on both leaf surfaces, cuticle 4 μm thick. Stomata always longitudinally orientated, arranged in short or long longitudinal rows. Stomatal apparatus averaging 59 (37–100) μm long and 47 (24–101) μm wide. Guard cells with wide, thickly cutinized semicircular dorsal plates and square-ended polar thickenings, sunken beneath ring of 2 polar plus 2 to 6 lateral subsidiary cells. Raised rectangular rim to stomatal pit, partially exposing guard cells and
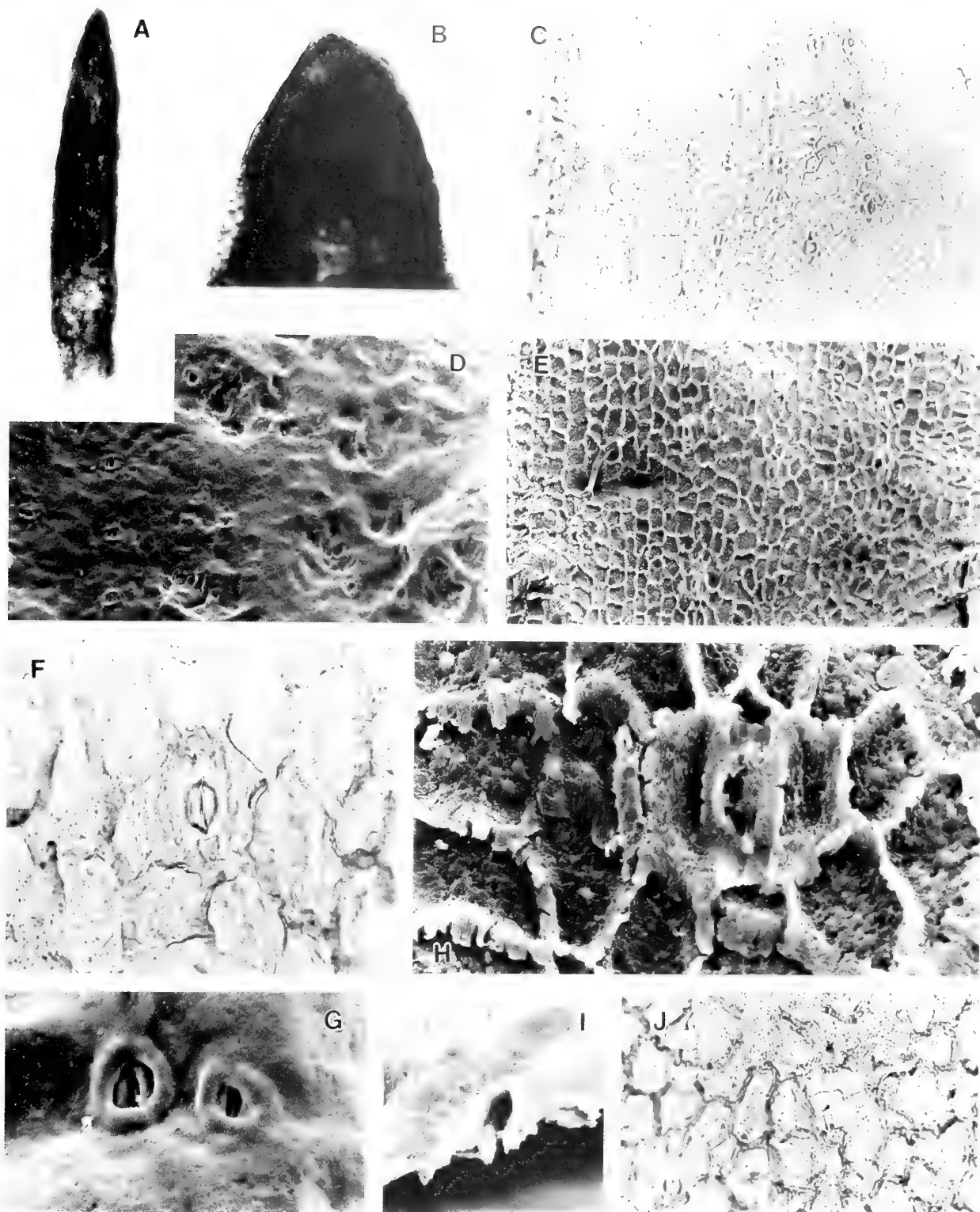
Fig. 1 A–J *Czekanowskia anguae* sp. nov. All from Wessex Formation, Dorset. **A–D, F, G, I, J** from Worbarrow Bay, **E, H** from Mupe Bay. **C–I** show upper cuticle. **A,** holotype, leaf with apex, V.64520, LM, × 10; **B,** mucronate apex of holotype, V.64520, LM, × 75; **C,** cuticle showing ordinary epidermal cells in longitudinal files, V.64521, LM, × 125; **D,** outer surface of cuticle, V.64521, SEM, × 125; **E,** inner surface of cuticle, V.64522, SEM, × 125; **F,** single stoma showing thickened rim and guard cell polar appendages, V.64523, LM, × 500; **G,** 2 stomata showing thickened rim and exposed stomatal aperture, V.64521, SEM, × 500; **H,** stoma viewed from inside, showing wide thickly cutinized dorsal plates of guard cells extending to tangential anticlinal walls of the lateral subsidiary cells, V.64522, SEM, × 750; **I,** cuticle showing stomata in files, V.64524, LM, × 250; **J,** transverse section through stoma, showing wide, thickly cutinized dorsal plates of guard cells and slit-like aperture, V.64525, SEM, × 750.
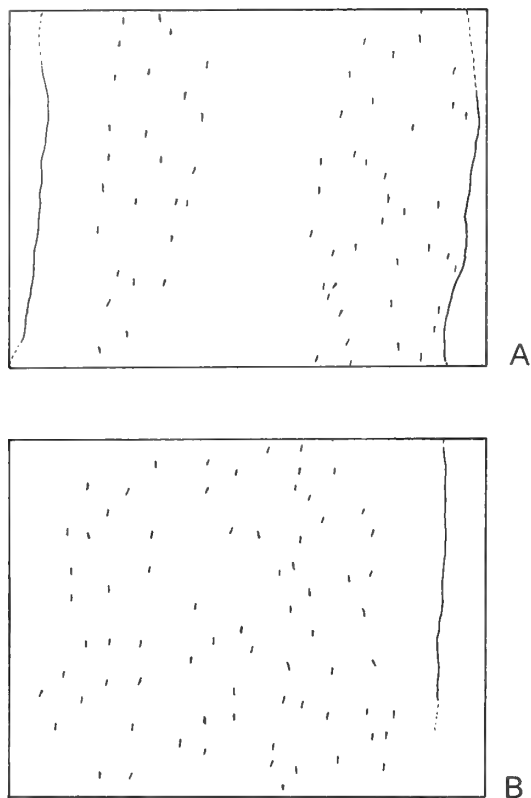
slit-like aperture. Ordinary epidermal cells less thickly cutinized than subsidiary cells, polygonal, mainly 4-sided, isodiametric or longitudinally elongate, arranged in longitudinal files; anticlinal walls weakly sinuous with ragged edges. Outer surface flat, lacking thickenings and papillae.

Stomata of upper surface averaging 47 (37–61) per mm², arranged in around 9 rows, sometimes avoiding median region of leaf; ordinary epidermal cells averaging 37 (17–71) μm long and 24 (10–47) μm wide. Stomata of lower surface averaging 79 (64–109) per mm², arranged in around 12 rows; ordinary epidermal cells averaging 31 (14–74) μm long and 25 (14–40) μm wide.

NAME.   After Angua, member of the Ankh-Morpork City Watch and she-werewolf in the Discworld novels of Terry Pratchett.

HOLOTYPE AND LOCALITY.   V.64520, Fig. 1A, the apical part of a leaf from the plant debris beds of Worbarrow Bay, Dorset. Wessex Formation; Hauterivian.

MATERIAL AND OCCURRENCE.   *Czekanowskia anguae* sp. nov. has been positively identified from the Wessex Formation of the English Wealden only. All the known material has been found as dispersed fragments, with good preservation, within 'plant debris beds' of Worbarrow and Mupe Bay in Dorset. Figs 1A–D, F, G, I, J; 2A, B; 3B, E show material from Worbarrow Bay. Figs 1E, H; 3A, C, D, F show material from Mupe Bay. Stratigraphical range: Hauterivian – Barremian.

DESCRIPTION AND DISCUSSION.   *Czekanowskia anguae* sp. nov. is the only species so far attributed to the genus *Czekanowskia* Heer

from the English Wealden. The few fragments recognised are of narrow needle shaped leaves (Fig. 1A) with a mucronate apex (Fig. 1B) but there is no evidence of differentiation into lateral and non-lateral areas, which would indicate the trapezoid cross-section shape described for species of this genus by Samylina & Kiritchkova (1991, 1993). It is only possible to separate the upper (Fig. 1C–I) and lower (Fig. 3A–F) cuticles of *C. anguae* on the basis of stomatal distribution and ordinary epidermal cell dimensions, although the two surfaces share closely similar features. The isodiametric to elongate ordinary epidermal cells are arranged in longitudinal files with those of the upper surface (Fig. 1C, E) somewhat more elongate than those of the lower (Fig. 3A, C). The anticlinal walls are weakly sinuous with ragged edges (Figs 1F, H; 3F). Stomata are arranged more or less in longitudinal rows on both surfaces (Figs 1C–E, I; 2A, B; 3A–C) with a much higher density on the lower surface. The guard cells are partially exposed revealing a slit-like aperture (Figs 1G; 3E) within the shallow, rectangular stomatal pits which have raised rims (the so-called 'Florin ring'); the outer surfaces of the leaf are otherwise smooth and featureless (Figs 1D; 3B). The ring of subsidiary cells consists of 2 to 4, and occasionally up to 6, lateral subsidiary cells and 2 smaller polar cells (Figs 1F, H; 3D, F).

The guard cells possess square-ended polar cuticular thickenings and wide, thickly cutinized semi-circular dorsal plates (Figs 1H, J; 3F) which appear to extend to the outer tangential anticlinal wall of the lateral subsidiary cells (Fig 1H). In many stomata, particularly those of the lower surface, cutinization of the inner anticlinal walls of the guard cells has produced a distinctive delicate oval structure on the inner surface (Fig 3F).

COMPARISON.   *Czekanowskia anguae* sp. nov. is the only species of this genus to be described from the English Wealden or indeed from any Lower Cretaceous deposit of western Europe. All other known *Czekanowskia* species of this age occur in the Lena and Amur provinces of the Siberian-Canadian palaeofloristic region, and Mongolia and Northern China (Samylina & Kiritchkova 1993). These species are also all assigned to the subgenus *Czekanowskia* along with *C. anguae*, as are all known species of younger age. Of the other Lower Cretaceous species *C. anguae* compares most closely to *Czekanowskia communis* Kiritchkova et Samylina from the Aptian of eastern Siberia (Samylina & Kiritchkova 1991). *C. communis* has a similar leaf width, lacks papillae and trichomes, and has stomatal pits with a raised, often rectangular, rim with the guard cells partially exposed. It differs from *C. anguae* in that both surfaces have a much lower stomatal density and more elongate ordinary epidermal cells.

Amongst Jurassic species, *Czekanowskia viminea* (Phillips) Kiritchkova et Samylina (subgenus *Czekanowskia*) from Yorkshire compares most closely with *C. anguae*, being similar in leaf width, ordinary epidermal cell shape and general stomatal structure but, *C. viminea* has more heavily cutinized subsidiary cells which are often papillate.

Ginkgoites leaf fragments occur with *C. anguae* in the same debris beds and fragments of the two species are of a similar general appearance. However, the *Ginkgoites* bears scattered, randomly orientated stomata with papillate subsidiary cells which are not distinctly polar or non-polar. They are thus easily separated microscopically and the *Ginkgoites* is described below as a new species.

Genus *PHOENICOPSIS* Heer

1876   *Phoenicopsis* Heer: 49.
1936b   *Phoenicopsis* auct. non Heer; Florin: 45.
1936b   *Stephanophyllum* Florin: 45.
1936b   *Culgoweria* Florin: 45.
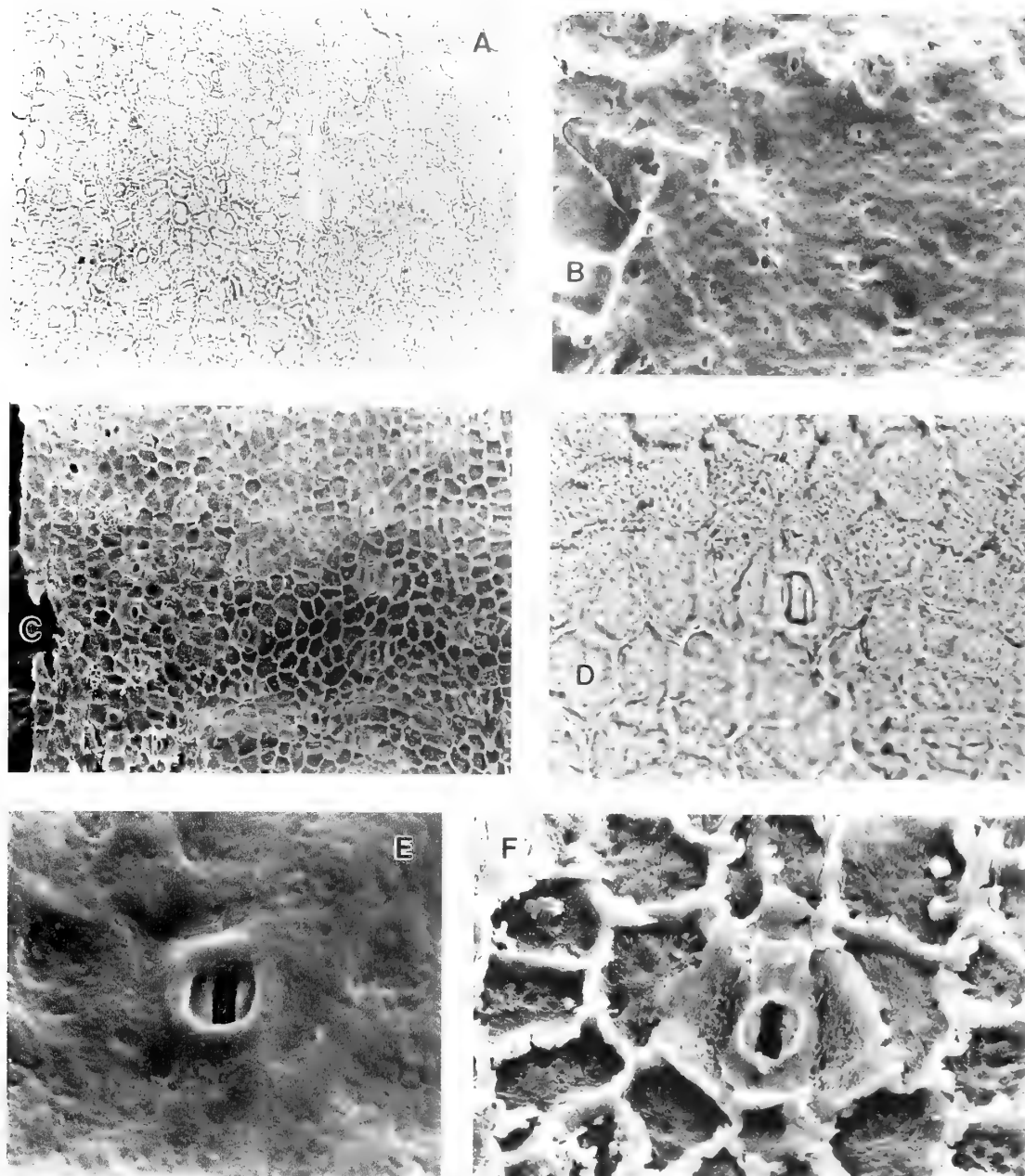
Fig. 3 A–F *Czekanowskia anguae* sp. nov. All lower cuticle, from Wessex Formation, Dorset. **B, E** from Worbarrow Bay. **A, C, D, F** from Mupe Bay. **A,** cuticle showing ordinary epidermal cells in longitudinal files. V.64522, LM, × 125; **B,** outer surface of cuticle showing stomatal rows. V.64521, SEM, × 125; **C,** inner surface of cuticle, V.64522, SEM, × 125; **D,** single stoma showing thickened rim and guard cell polar appendages, V.64522, LM, × 500; **E,** stoma viewed from outside, showing thickened rectangular rim and partially exposed guard cells, V.64521, SEM, × 750; **F,** stoma viewed from inside, showing wide, thickly cutinized dorsal plates and polar appendages of guard cells, also showing distinctive cutinization of the inner anticlinal walls of the guard cells producing delicate oval structure, V.64522, SEM, × 750.

1936b   *Windwardia* Florin: 45.
1972   *Phoenicopsis* Heer; Samylina: 58.
1987   *Phoenicopsis* Heer; Sun: 685.

TYPE SPECIES.   *Phoenicopsis angustifolia* Heer 1876: 51; pl.1, fig.1d; pl.2, fig.3b (cuticle figured by Florin 1936a; pl.36, figs.4,5).

DIAGNOSIS.   [slightly emended from Heer, 1876: 49] Foliage leaves borne in bundles on short caducous shoots which also bear small persistent leaves. Foliage leaves narrowly wedge-shaped with no distinction between petiole and lamina, undivided. Single vein at leaf base dichotomising into numerous parallel veins. Resin bodies absent.

DISCUSSION.   The genus *Phoenicopsis* is used here in the sense of Heer (1876) and later that of Samylina (1972: 58) which makes it

readily distinguishable from all other Czekanowskiales by its gross form, thus differing from the generic proposals of Florin (1936b). Florin (1936b: 45) suggested that bundles of leaves agreeing in gross morphology with Heer's (1876) generic diagnosis for *Phoenicopsis* should be split into four genera: *Phoenicopsis* for leaves whose cuticular structure was unknown; *Stephanophyllum* for those with hypostomatic foliage leaves; *Culgoweria* for amphistomatic leaves with stomata in files; *Windwardia* for amphistomatic leaves with stomata in bands. In 1972, Samylina again revised the status of the genus *Phoenicopsis* such that *Stephanophyllum*, *Culgoweria* and *Windwardia* were abandoned as distinct genera but with *Culgoweria* and *Windwardia* retained within *Phoenicopsis* as sub-generic taxa or sections. The genus *Phoenicopsis* Heer *sensu* Samylina is recognisable from gross form alone, whilst the sections or sub-genera are distinguished by differences in stomatal distribution.

Key for identifying sections within the genus *Phoenicopsis*:
1.a) Leaf hypostomatic.   *Phoenicopsis* (section *Phoenicopsis*)
1.b) Leaf amphistomatic.   go to 2
2.a) Stomata in files.   *Phoenicopsis* (section *Culgoweria*)
2.b) Stomata in bands.   *Phoenicopsis* (section *Windwardia*)

Samylina's work removes the artificial category set up by Florin for leaves whose cuticles are unknown and brings *Phoenicopsis* into line with other Czekanowskialean genera which were already distinguished on gross form alone. Thus cuticular features are reserved for distinctions at sub-generic and species level throughout the order. Sun (1987) discussed and adopted Samylina's scheme in describing three new species of *Phoenicopsis* from the Mesozoic of northeast China, all referred to the subgenus *Culgoweria*. The new species of *Phoenicopsis* described below is also attributable to the sub-genus *Culgoweria* as defined above.

Phoenicopsis rincewindii sp. nov.   Figs 4–6

DIAGNOSIS.   [based on leaf fragments only] Parallel-sided leaf 2–5 mm wide [base and apex unknown]. Veins indistinct, at least 4 per leaf.

Thicker cuticle (?upper) 5–8 µm thick with stomata arranged in longitudinal files between veins, density about 20 per mm², longitudinally or obliquely orientated. Stomatal apparatus on both surfaces 55–90 µm long × 35–60 µm wide; stomatal pit square or rectangular with 4–6 subsidiary cells in a distinct ring around pit; inner anticlinal walls forming thickened rim to pit; lateral subsidiary cells usually with solid papillae projecting over pit; periclinal walls slightly thicker than on ordinary epidermal cells. Guard cells slightly sunken beneath subsidiary cells; dorsal plates thinly cutinized, axe-head-shaped, faint radiating striae on inside; inner anticlinal walls shallowly cutinized. Encircling cells usually absent. Ordinary epidermal cells arranged in longitudinal files, generally four-sided, elongate 38–112

µm long × 10–20 µm wide, end walls transverse or oblique. Anticlinal walls narrow, about 1 µm wide, straight or slightly sinuous and pitted. Longitudinal cutinized ridges present over surface of some cells. Inside surface of periclinal walls finely pitted. Papillae absent from ordinary epidermal cells. Hypodermis absent. Thinner cuticle with stomata arranged in longitudinal files over whole surface, not avoiding veins, density typically 70–76 per mm², longitudinally or obliquely orientated. Ordinary epidermal cells arranged in longitudinal files, generally four-sided; those between stomatal files elongate, typically 50–70 µm long × about 10 µm wide, end walls transverse or oblique; cells within stomatal files slightly elongate or isodiametric, 10–57 µm long × 10–23 µm wide, end walls transverse, rarely oblique. Slight median thickenings or ridges present over surface of most cells. Inside surface of periclinal walls finely pitted. Anticlinal walls narrow, about 1 µm wide, straight or pitted and appearing slightly sinuous.

NAME.   After Rincewind, ineffective wizard of the Unseen University in the Discworld novels of Terry Pratchett.

HOLOTYPE AND TYPE LOCALITY.   V.64527, a portion of leaf from Fairlight, near Hastings, East Sussex. Figs 4B, D, E, H, I, J; 6B, D, E. Ashdown Beds Formation, Berriasian.

MATERIAL AND OCCURRENCE.   *Phoenicopsis rincewindii* sp. nov. is known only from dispersed material from Fairlight, near Hastings, East Sussex. Ashdown Beds Formation, Berriasian.

DESCRIPTION.   The remains of the largest leaf fragments of *Phoenicopsis rincewindii* recognised so far are shown in Fig. 4A, B with the latter opened up to show both leaf surfaces. Both are photographed after the removal of part of their length for SEM cuticle preparations. The rather thinner cuticle on the left of Fig. 4B is presumed to be from the lower surface of the leaf. Apart from its thickness, this cuticle (Figs 6A–E) only differs from that of the other surface (Figs 4C–I) in having more stomata per mm² and having somewhat less elongate epidermal cells. Otherwise most features are more or less similar on both cuticles. Fig. 4E, I, J shows the longitudinal cuticular ridges over the epidermal cells of the upper surface, some restricted to one cell but often extending along a file of cells. Figs 5C and 6B show the lower surface of the leaf which is less strongly ridged and thus thinner overall. The arrangement of the stomata in files on the lower surface can be seen in Figs 4B (left) and 6A. It is less apparent for the upper surface with sparser stomata (Fig. 4C) but this is partly because of the strong longitudinal wrinkling (Fig. 4B, right) which is a preservational feature, probably associated with a tendency for the leaf surface to become furrowed between the veins (Fig. 4E).

A high frequency of paired stomata is noted with two stomata either sharing one polar subsidiary cell, or with their polar subsidiary cells sharing an end wall as in the pair of stomata shown in Figs 5C

Fig. 4 A–J   *Phoenicopsis rincewindii* sp. nov. **A, B, D,** both leaf surfaces; **C, E–J,** thicker (? upper) leaf cuticle. **A,** longest fragment of leaf showing whole width, V.64526, LM, × 15; **B, holotype,** leaf fragment opened up to show both surfaces, thicker cuticle on right, V.64527, LM, × 25; **C,** sparse stomata avoiding vein tracts; ordinary epidermal cells elongate, arranged in well-defined longitudinal files, V.64526, LM, × 125; **D, holotype,** inside view of opened up leaf with elongate cells of leaf margin in centre (arrow), thicker cuticle on left with stomata between vein tracts, thinner cuticle with higher stomatal density on right, V.64527, SEM, × 125; **E, holotype,** outer surface showing strong longitudinal wrinkling and lateral compression, probably with veins forming the ridges, V.64527, SEM, × 125; **F,** stoma showing subsidiary cells with more thickly cutinized periclinal walls than surrounding cells and pit overhung by papillae of subsidiary cells, V.64526, LM, × 500; **G,** cuticle viewed from the inside showing pitted anticlinal walls to ordinary epidermal cells and stoma with two lateral and two polar subsidiary cells, V.64527, SEM, × 500; **H,** inside view of a stoma showing axe-head-shaped dorsal plates to guard cells with fine radiating striae, V.64527, SEM, × 1000; **I, J, holotype,** cuticle viewed from the outside showing ordinary epidermal cells with longitudinal ridges; ridges in Fig. I ending abruptly adjacent to stoma with smooth subsidiary cell surface and papillae overhanging pit, V.64527, SEM, × 500.
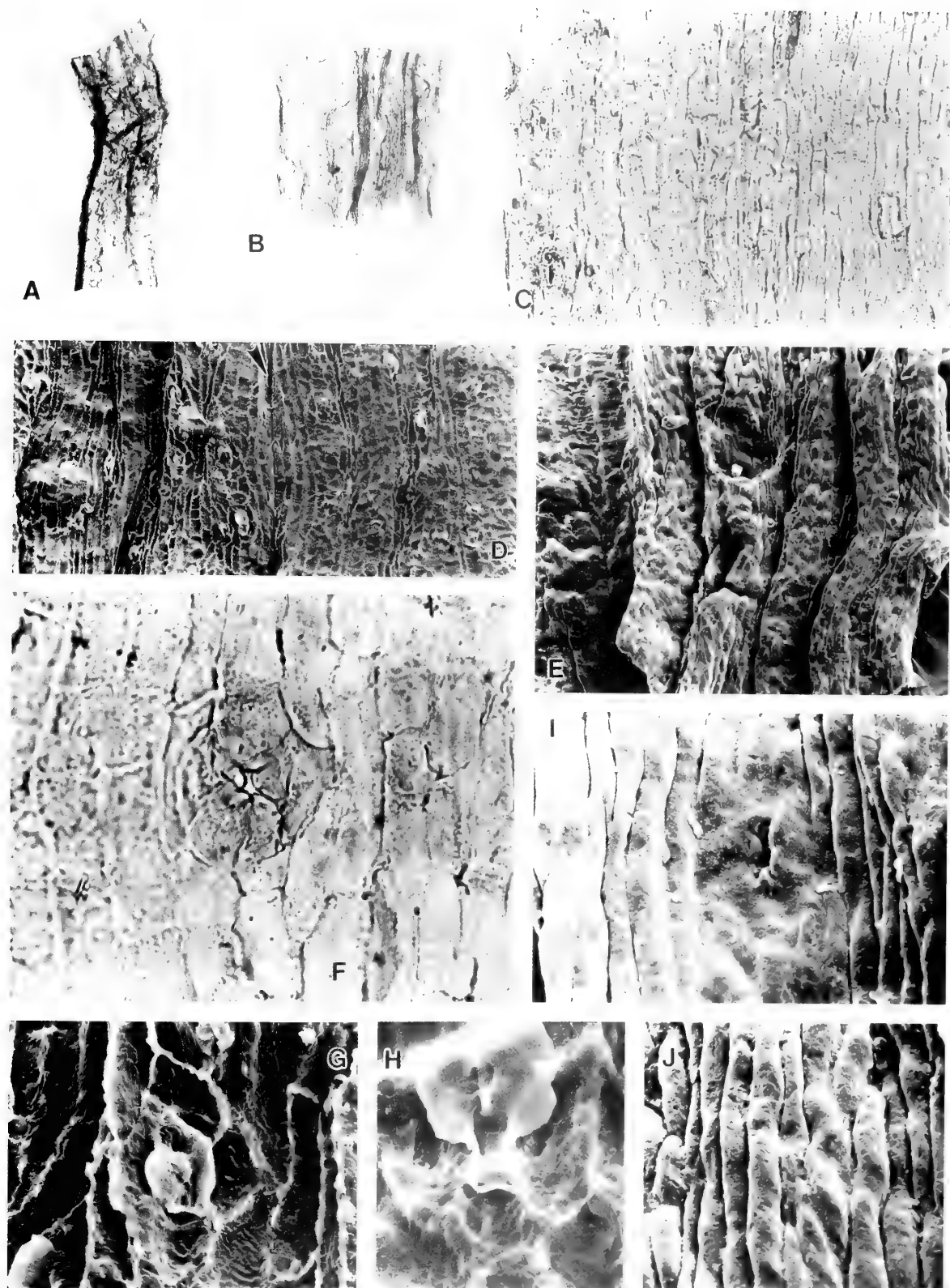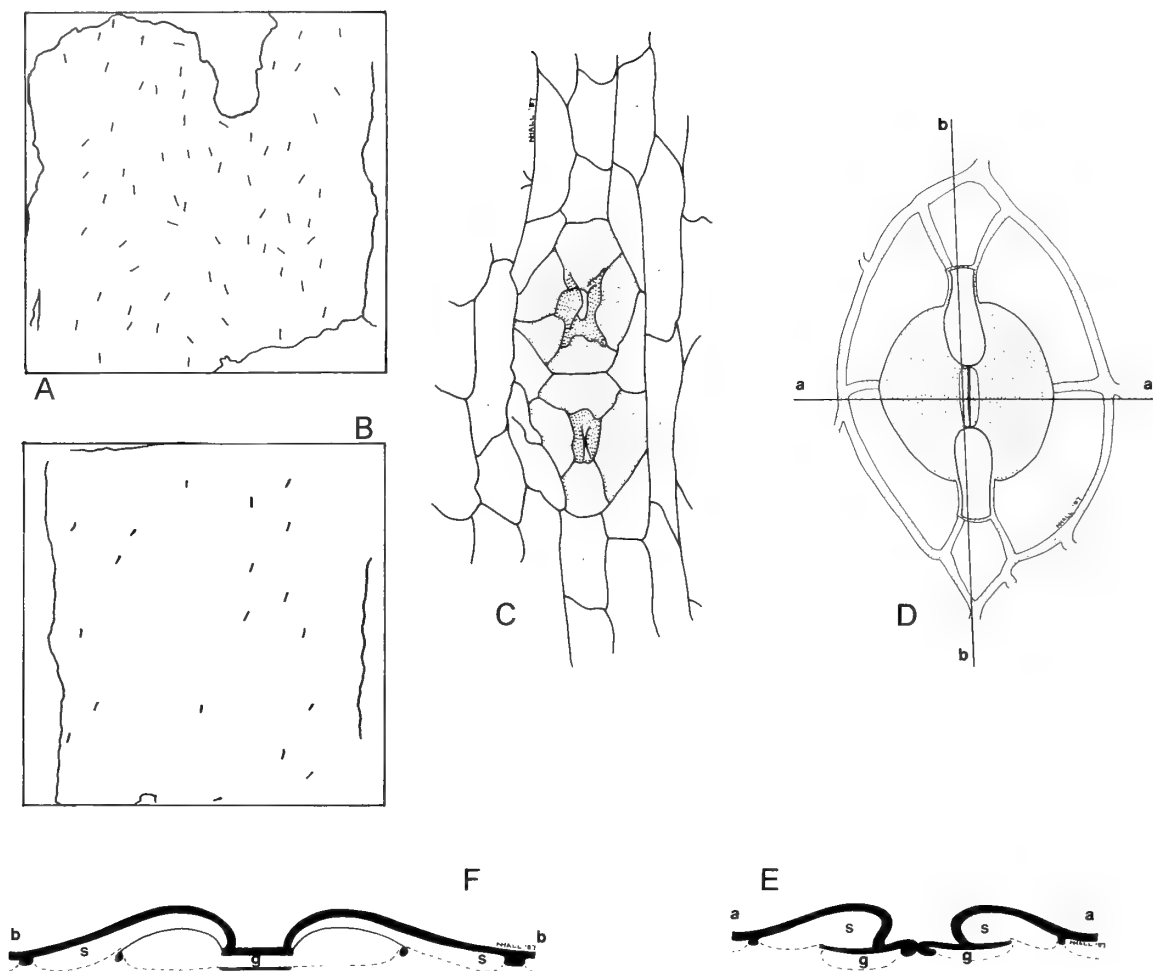
Fig. 5 A–F   *Phoenicopsis rincewindii* sp. nov. **A, B,** stomatal distribution and orientation across width of leaf. Same leaf margin on right of Fig. A and left of Fig. B. **A,** presumed lower (thinner) cuticle, **B,** presumed upper (thicker) cuticle, both V.64526, × 50; **C,** stomatal pair from the lower cuticle, V.64526, × 400; **D–F,** stylised stoma based on observations in the SEM, approximately × 1000; **D,** viewed from inside of cuticle; **E,** transverse-vertical section along line a–a; **F,** longitudinal-vertical section along line b–b; g –guard cell; s – subsidiary cell.

and 6C. In the light microscope, the subsidiary cells appear darker than those of the general epidermis (Figs 4F, 5C, 6A, C) because of the greater thickness of their surface walls. In many Czekanowskiales this appearance is caused by the cutinization of the inner periclinal walls, but the SEM has, as yet, afforded no evidence of inner periclinal cutinization on the subsidiary cells of *P. rincewindii* (Fig. 4G, H). The typical arrangement of the subsidiary cells in this species, a single polar subsidiary cell at each end of the stomatal pit and one or two lateral subsidiary cells on each side, is shown in Figs 4G, 5C, D. The thickened inner anticlinal walls of the subsidiary cells frequently form flat papillae on the lateral cells protruding over the stomatal pit (Figs 4F, I; 5C; 6C, D). The characteristic axe-head shaped outline of the guard cell-dorsal plates is shown in Figs 4H and 5D

DISCUSSION.   *P. rincewindii* sp. nov. exhibits the following czekanowskialean features: linear leaves; stomata in files; subsidiary cells with thicker periclinal walls than other epidermal cells. It is assigned to the genus *Phoenicopsis* rather than *Czekanowskia* because

of the numerous parallel veins, and to the sub-genus *Culgoweria* because the stomata are on both leaf surfaces and arranged in files (see generic discussion above).

COMPARISON.   The general arrangement of the stomata and the common occurrence of stomatal pairs in *P. rincewindii* is reminiscent of *Phoenicopsis steenstrupii* Seward (1926) from the Lower Cretaceous of western Greenland, which is also attributable to the subgenus *Culgoweria*. However, material of *P. steenstrupii* was reinvestigated (Hall 1987) and the two species were found to be easily distinguished by differences in stomatal densities on both surfaces, stomatal orientation, nature of the anticlinal cell walls and length of ordinary epidermal cells.

The extremely limited number of specimens of *P. rincewindii* prevents useful comparison of gross morphology with the many other species of *Phoenicopsis* described in particular by Samylina (1972), Sun (1987) and Zhou & Zhang (1998), and this must await further discoveries in the debris bed material.
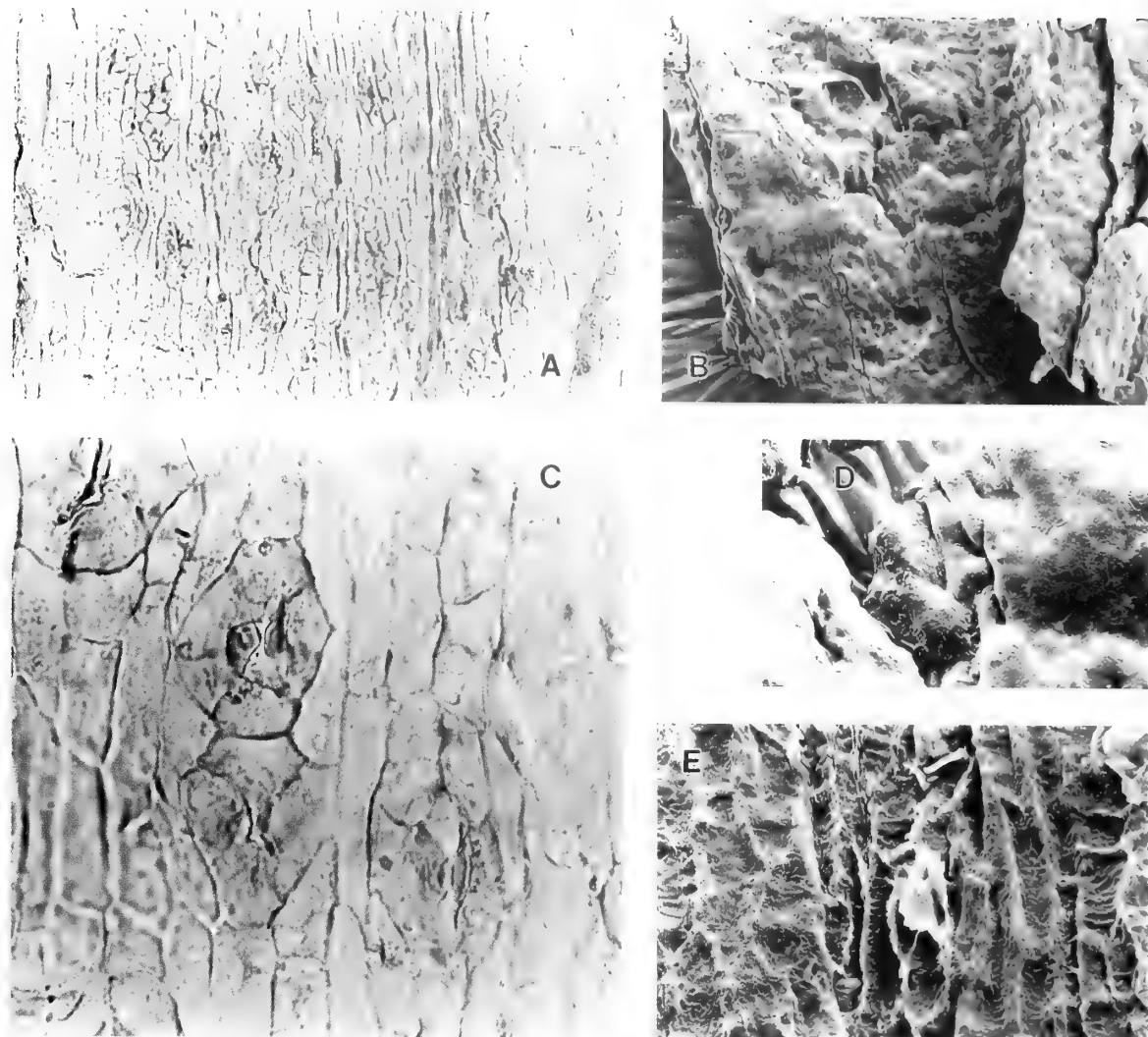
Fig. 6 A–E   *Phoenicopsis rincewindii* sp. nov. All thinner (? lower) cuticle. **A,** widely distributed stomata scarcely avoiding veins, V.64526, LM, × 125; **B, holotype,** outer surface less strongly ridged than that of thicker cuticle seen in Fig. 4, V.64527, SEM, × 500; **C,** stomata showing subsidiary cells with more thickly cutinized periclinal walls than surrounding cells and pits overhung by papillae of lateral subsidiary cells; details of adjacent stomata on left shown in Fig.5C, V.64526, LM, × 500; **D,** outside view of a stoma showing elongate pit overhung by subsidiary cellpapillae, V.64527, SEM, × 500; **E,** cuticle viewed from the inside showing pitted anticlinal walls to ordinary epidermal cells and stoma, V.64527, SEM, × 500.

Order **GINKGOALES**
Genus *GINKGOITES* Seward

1919   *Ginkgoites* Seward: 10. [formal diagnosis not given]
1935   *Ginkgoites* Seward; Harris: 48
1936a *Ginkgoites* Seward; Florin: 105
1968   *Ginkgoites* Seward; Tralau: 67
1972   *Ginkgoites* Seward; Krassilov: 24
1974   *Ginkgoites* Seward; Harris & Millington: 4. [dropped in favour of *Ginkgo* L.]
1997   *Ginkgoites* Seward; Zhou: 190
1999   *Ginkgoites* Seward; Watson *et al*: 721

TYPE SPECIES.   *Ginkgo obovata* Nathorst 1886: 93, pl. 20, fig. 3. [Cited by Andrews, 1970]

DIAGNOSIS.   [emended by Watson *et al* 1999: 721] Fossil leaves occurring singly. Petiole distinct, enlarging abruptly at its top to form lamina. Lamina with straight lateral margins, distal margin forming arc of a circle; shallowly to deeply incised. Veins repeatedly dichotomising, ending separately in distal margin. Cuticle where known with haplocheilic stomata.

REMARKS.   Fossil ginkgoalean leaf genera were discussed at length by Watson *et al* (1999), both in their historical context and in the light of recent discoveries (Kimura *et al* 1983; Zhou & Zhang 1989, 1992; Zhou 1991, 1997; Zhao *et al* 1993; Czier 1998) with two major difficulties highlighted. First of all, the problem of dealing with leaves which show wide variation in morphology within a single species is considerable. This is a difficult problem for whole leaf specimens as well as fragmentary debris material. Secondly, the argument against using the genus *Ginkgo* L. for fossil leaves in which reproductive structures are completely unknown was

discussed. The disadvantage of this usage has recently been illustrated by Zhou & Zhang (1992) with their discovery of ginkgoalean ovuliferous organs so different from those of *G. biloba* as to require the erection of a new genus *Yimaia* Zhou & Zhang (1992). Following Zhou (1997), Watson *et al* (1999) readopted *Ginkgoites* Seward as a form- or organ-genus in the redescription of the leaf species *Ginkgoites brauniana* (Dunker) Watson *et al* and *Ginkgoites pluripartita* (Schimper) Seward, from the Lower Cretaceous Wealden facies of Germany. This usage seems to us even more relevant to the

naming of the extremely fragmentary material described below as three new species of *Ginkgoites* Seward.

Ginkgoites weatherwaxiae sp. nov.   Figs 7–11

1976   29 Gink GkC Oldham (Code used instead of Linnean binomial): 462, pl. 69, figs 7, 8; pl. 70, figs 1, 2.

DIAGNOSIS.   [based on leaf fragments only] Leaf petiole 0.5 mm wide, expanding into lamina deeply divided into primary segments,

Fig. 7 A–H   *Ginkgoites weatherwaxiae* sp. nov. **A,** leaf segment with rounded apex and numerous resin bodies, V.64528, LM, × 15; **B,** large leaf segment with mucronate apex, V.64529, LM, × 10; **C, holotype,** branched leaf fragment showing two dichotomies, with numerous resin bodies, particularly along left margin. V.64530, LM, × 10; **D,** forked apex of branched leaf fragment with pointed growing tips, V.64531, LM, × 20; **E,** unbroken mucronate apex, V.64532, SEM, × 50; **F,** apex of leaf segment in Fig. B with broken mucronate tip, V.64529, LM, × 50; **G,** leaf segment showing bite which has pierced both surfaces, V.64533, LM, × 25; **H,** edge of bite in Fig. G showing evidence of reaction after damage, V.64533, LM, × 100.
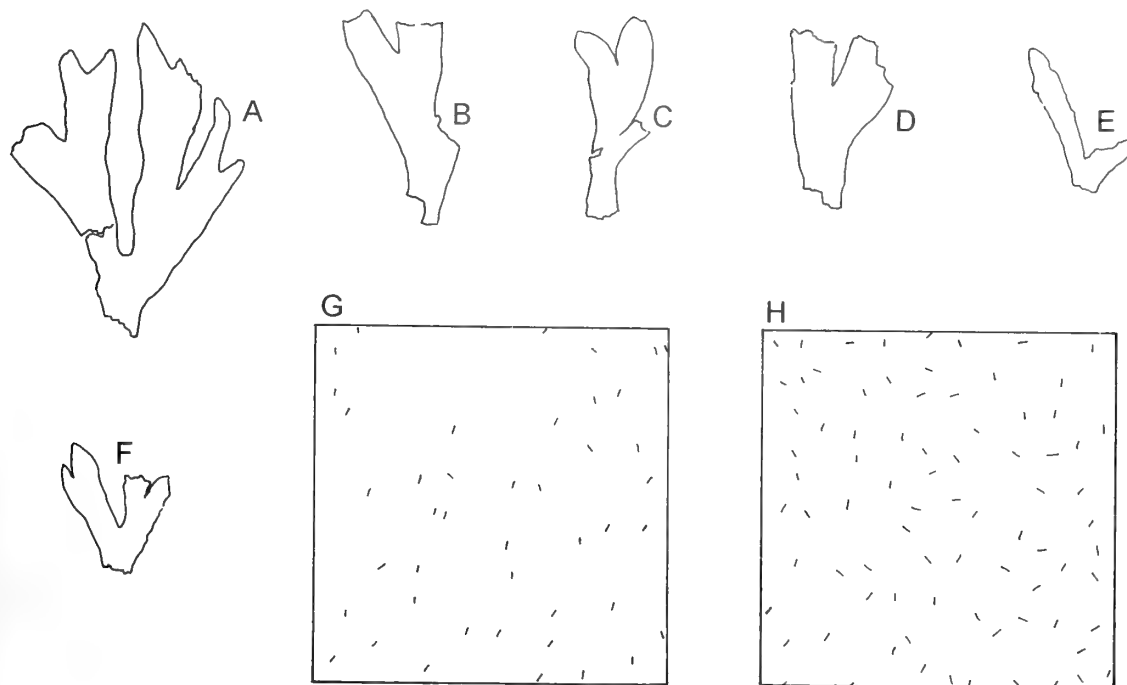
Fig. 8 A–H *Ginkgoites weatherwaxiae* sp. nov. **A–F** Branched leaf fragments showing up to three successive dichotomies, all × 5. **A**, V.64534; **B**, **holotype**, seen also in Fig. 7C, V.64530; **C**, V.64535; **D**, V.64536; **E**, V.64537; **F**, V.64531; **G**, stomatal distribution and orientation for upper surface, V.64538, × 50; **H**, stomatal distribution and orientation for lower surface, V.64539, × 50.

split by at least 3 successive dichotomies at intervals of at least 3.5 mm. Ultimate lobes at least 15 mm long, 3 mm wide, of constant width, apices rounded or mucronate. [Veins unknown.] Resin bodies numerous, circular, 50–300 µm in diameter.

Cuticle 6 µm thick, stomata present on both leaf surfaces, scattered. Stomatal apparatus elliptical in outline; guard cells with thickly cutinized semi-circular dorsal plates and inner anticlinal walls, sunken beneath ring of 4–7, usually 6, thickly cutinized subsidiary cells which surround stomatal pit; pit rim thickened, usually with one hollow papilla per subsidiary cell overhanging guard cells. Ordinary epidermal cells less thickly cutinized than subsidiary cells, polygonal, mainly 4-sided, isodiametric or longitudinally elongate, arranged in longitudinal files; anticlinal walls straight, sometimes pitted. Stomata of upper surface averaging 30 (13–58) per mm²; stomatal apparatus typically 80 (54–111) µm long and 60 (40–81) µm wide; pit oval or slit like; aperture usually longitudinally orientated. Ordinary epidermal cells averaging 35 (10–67) µm long and 21 (10–40) µm wide; outer surface usually flat, very occasionally patches of cells with longitudinal, ridge-like thickenings or small papillae in centre or at end of each cell.

Stomata of lower surface averaging 64 (42–91) per mm²; stomatal apparatus typically 70 (40–88) µm long and 60 (40–78) µm wide; pit circular to oval; aperture randomly orientated. Ordinary epidermal cells averaging 27 (10–64) µm long and 22 (10–40) µm wide; more longitudinally elongate at margins; outer surface flat, lacking thickenings and papillae.

Petiole approximately 0.5 mm wide with distinct regions of upper and lower cuticle; when dissected, lower cuticle forming band 0.4 mm wide, upper cuticle 1.1 mm wide. Stomata scattered on both surfaces, stomatal apparatus as for lamina. Ordinary epidermal cells of upper surface typically 4-sided, 54 (30–84) µm long and 14 (7–24) µm wide, arranged in longitudinal files. Stomata 73 (34–105) µm

long and 51 (34–61) µm wide, longitudinally orientated, averaging 11 per mm². Ordinary epidermal cells of lower surface polygonal, mostly 4-sided, 40 (17–67) µm long and 19 (10–34) µm wide, arranged in vague longitudinal files. Stomata 69 (52–81) µm long and 60 (51–74) µm wide, randomly orientated, averaging 31 per mm².

NAME. After Granny Weatherwax, formidable witch of Lancre in the Discworld novels of Terry Pratchett.

HOLOTYPE AND TYPE LOCALITY. V.64530, Figs 7C, 8B, a dispersed leaf fragment from the plant debris beds of Worbarrow Bay, Dorset. Wessex Formation; Hauterivian.

MATERIAL AND OCCURRENCE. All specimens of *Ginkgoites weatherwaxiae* sp. nov. figured here have been found as dispersed fragments, with good cuticle preservation, within the plant debris beds of the Wessex Formation at Worbarrow Bay, Dorset. This species was also identified by Oldham (1976) in samples from Swanage in Dorset, Brook Chine on the South West coast of the Isle of Wight, and from the Ashdown Beds Formation at Hastings and Galley Hill in East Sussex. Stratigraphical range: Berriasian – Barremian.

DESCRIPTION AND DISCUSSION. The fragments of *Ginkgoites weatherwaxiae* sp. nov. recognised so far indicate the presence of a lamina which is deeply divided into narrow dichotomizing segments (Figs 7A–D; 8 A–F) and a distinct petiole (Fig. 9A) but it has not yet proved possible to reconstruct a whole leaf. Fig. 7A, B shows typical terminal segments; Fig. 7C, D and Fig. 8A–F show branching of primary lobes into smaller terminal segments. The segment apices vary considerably, being rounded (Fig. 7A), blunt (Fig. 8C), pointed (Figs 7B, 8F) and even forked (Fig. 7D). The pointed type of apex, such as that of the specimen in Fig. 7B, F is sometimes mucronate
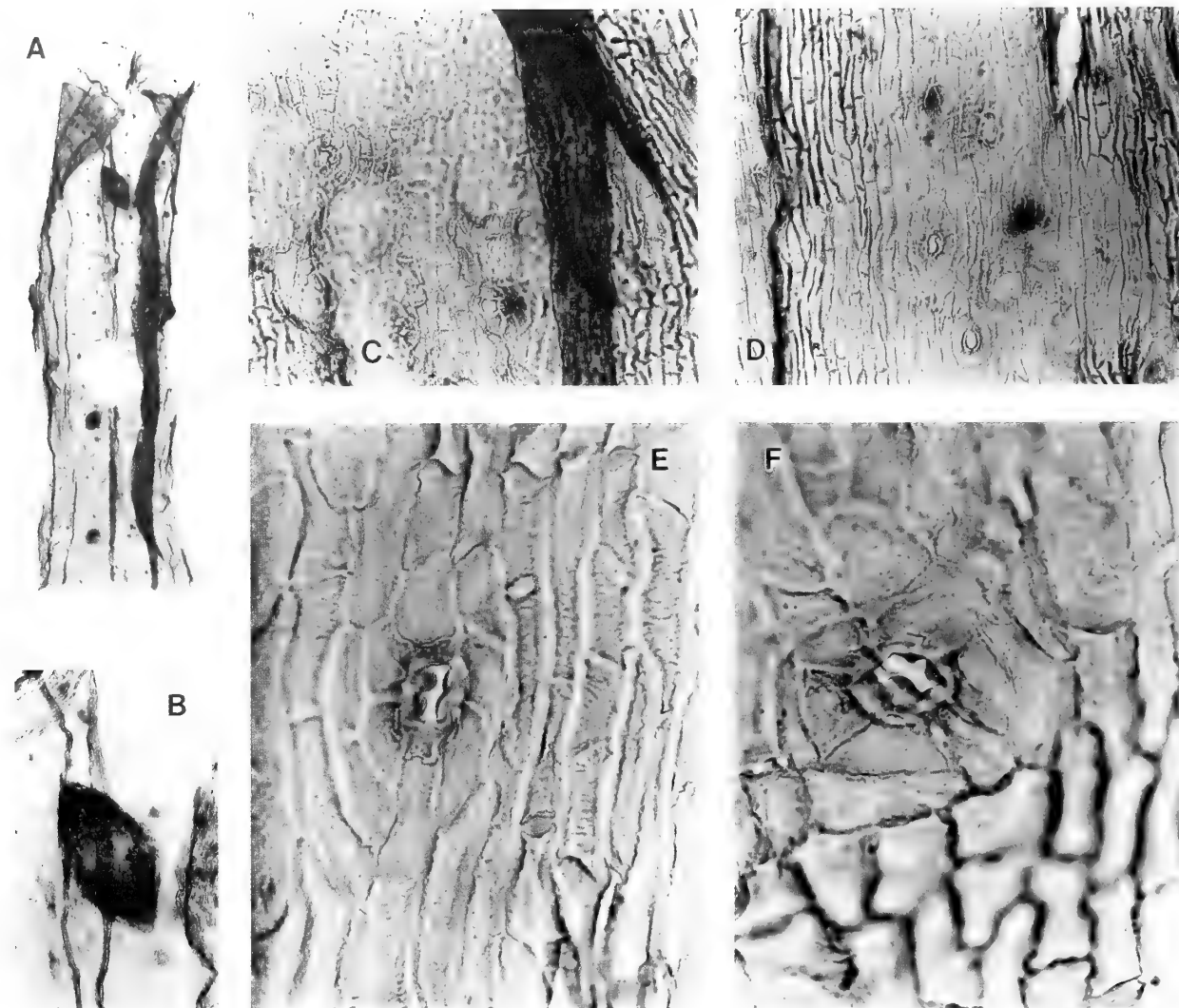
Fig. 9 A–F   *Ginkgoites weatherwaxiae* sp. nov. All light micrographs of petiole specimen V.64540. **A,** fragment of petiole, dissected and opened out, showing large round bite-mark and resin bodies, × 15; **B,** large, spindle-shaped resin body present in petiole, seen also in upper part of Fig. A, × 50; **C,** cuticle of upper surface, showing ordinary epidermal cells in rows and distribution of stomata, × 125; **D,** cuticle of lower surface, showing elongate ordinary epidermal cells and stomatal distribution, × 125; **E,** single elongate, longitudinally aligned, stoma on upper surface, × 500; **F,** inconspicuous stoma on lower surface, × 500.

(Fig. 7E) but the extreme tip is often broken or missing. This feature is commonly found in fossil conifers and its significance has been speculated upon and discussed by various authors, most recently by Watson & Harrison (1998) in relation to *Pseudotorellia linkii* which is described below.

The petiolate nature of the *G. weatherwaxiae* leaf is recognised from the cuticle similarity in isolated specimens (Fig. 9A) with typical petiole characters such as narrow, more elongate cells (Fig. 9C, D), low stomatal densities and small stomata (Fig. 9E, F). Unfortunately, in none of the specimens is there any indication of how the top of a petiole widens and passes into the basal part of the leaf lamina. The petiole in Fig. 9A, and the leaf segment in Fig. 7G are particularly interesting in showing what appears to be animal (presumably arthropod) damage. The hole in the cuticle in Fig.7G, H shows clear evidence of reaction to the damage and signs of repair around the edges of the damage (Fig. 7H) which involves both

surfaces of the leaf. Figs 12D, 14D show what is possibly post-mortem insect damage in a *Ginkgoites* leaf and are discussed further below. In recent years study of such animal traces in fossil plants have considerably increased with a view to gaining important information about the evolution of these relationships (Scott & Titchener 1999). Insects described from the English Wealden (Jarzembowski 1995) include hemipterans, or bugs, which have mouthparts modified into a tubular beak for piercing and sucking. Despite the general resistance of *Ginkgo biloba* to pests, infestation by homopterous hemipterans is well known (Honda 1997) and the presence in the Lower Weald Clay (Hauterivian) of *Penaphis woollardi* Jarzembowski, thought to belong to an extant lineage of gymnosperm-feeding aphids (Jarzembowski 1989), is an intriguing possibility. The sizes of the bites or punctures in these leaves, at up to 1 mm (Figs 9A; 12D; 14D), are somewhat large for confident attribution to aphids (Jarzembowski pers. comm. 2000) and are more likely to be
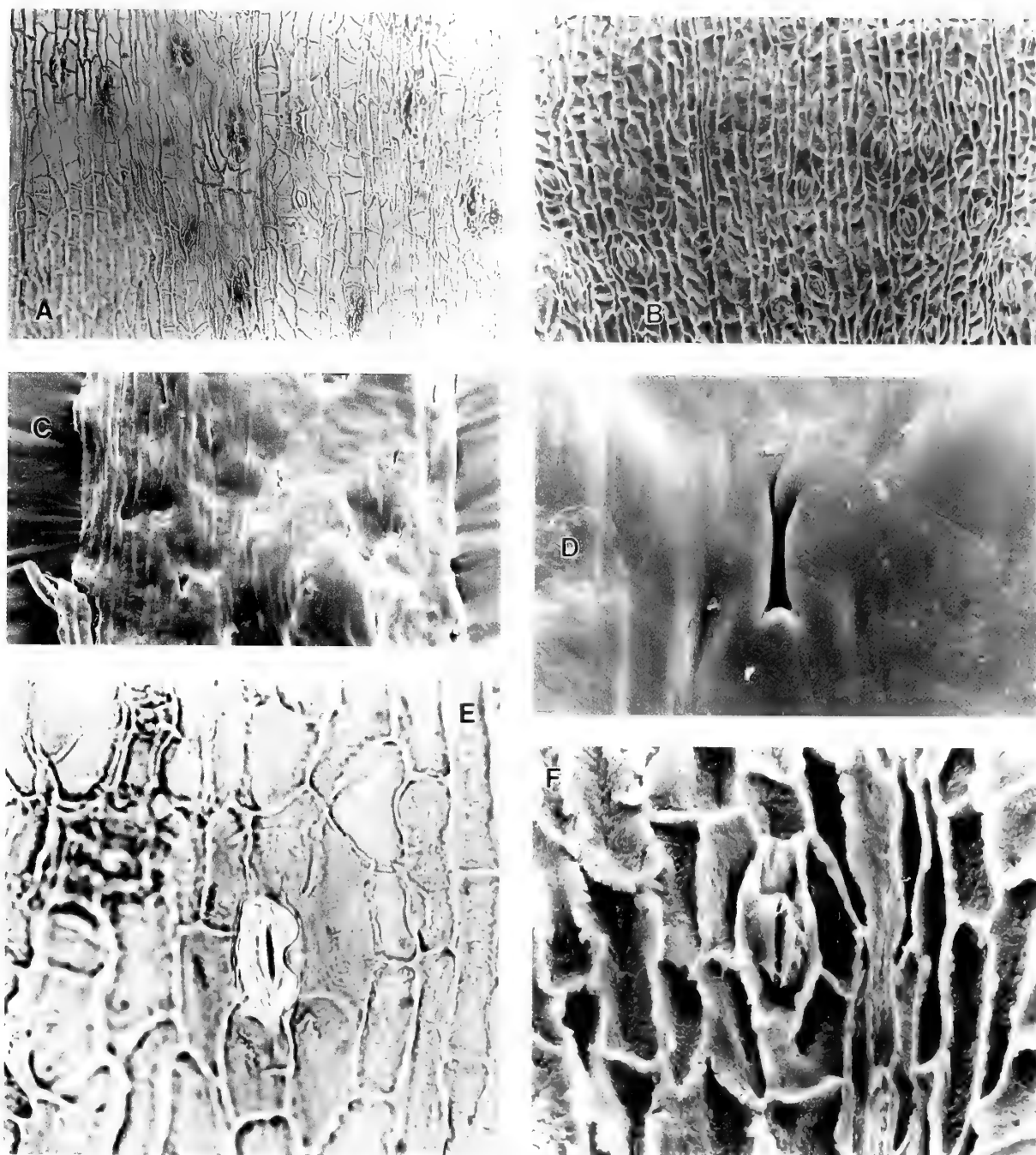
Fig. 10 A–F *Ginkgoites weatherwaxiae* sp. nov. All cuticle of upper surface of leaf. **A,** stomatal distribution and arrangement of ordinary epidermal cells in rows, V.64541, LM, × 125; **B,** inner surface of cuticle showing stomatal distribution and arrangement of ordinary epidermal cells in rows, V.64542, SEM, × 125; **C,** outer surface of cuticle showing ridging on left, V.64542, SEM, × 125; **D,** outer surface of cuticle with slit-like stomatal pit, V.64542, SEM, × 750; **E,** single stoma showing ring of subsidiary cells with one papilla overhanging the stomatal pit, V.64541, LM, × 750; **F,** single stoma viewed from inside showing guard cells with thickly cutinized semi-circular dorsal plates and inner anticlinal walls around the stomatal slit, V.64542, SEM, × 750.

the work of various leaf litter feeders. However, damage by aphids is well known to introduce infestations of fungi and bacteria, with subsequent decay and enlargement of the puncture. Damage comprising small circular perforations and even semicircular 'nibbles' can only be caused by mandibulate insects such as beetles (Coleoptera) and not haustellate ones such as bugs. Recent leaf

beetles and weevils commonly produce holes in leaves of seed plants. Beetles are the most common insect order in the Wealden and include plant feeders (Jarzembowski 1995). Fossil damage such as that on the leaves of *G. weatherwaxiae* can be referred to the ichnogenus *Phagophytichnus*.

The stomatal apparatus of both surfaces is typically oval in outline
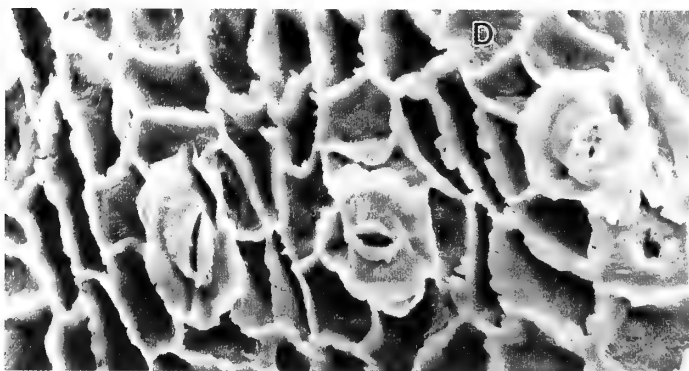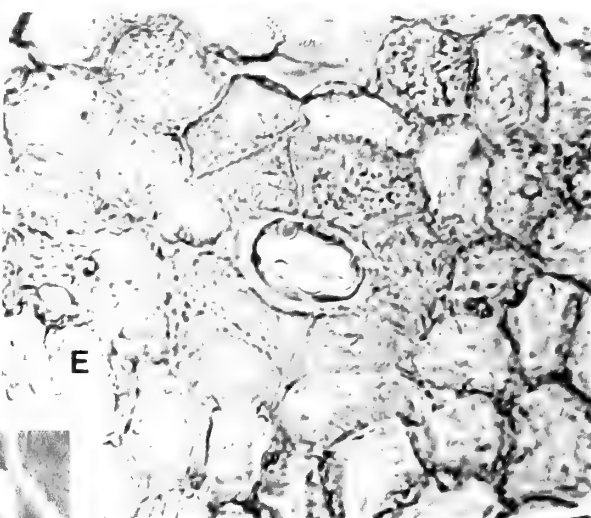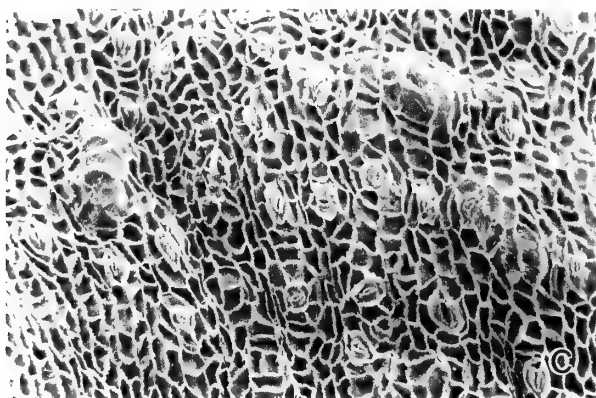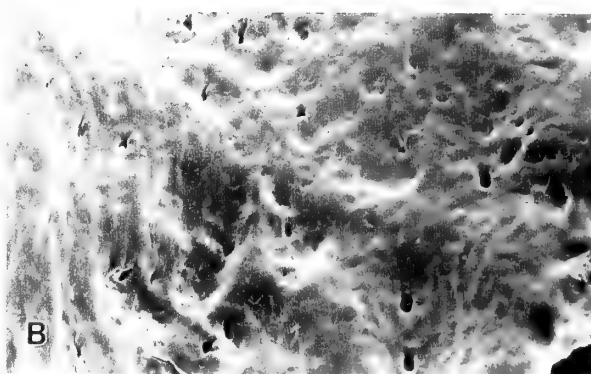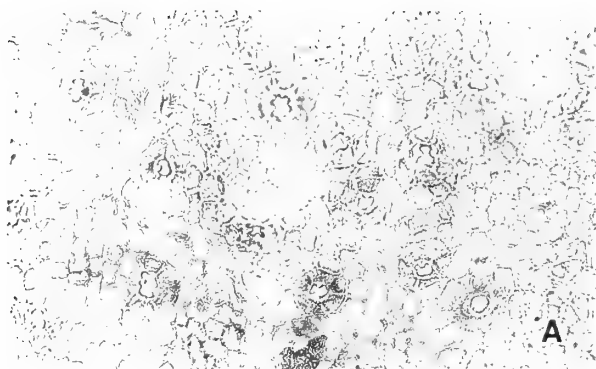
(Figs 10E, F; 11E, H) and has guard cells with strongly cutinized dorsal plates (Figs 10F; 11D, H) forming the floor of the stomatal pit. The guard cells are also thickly cutinized along the part of the inner anticlinal wall adjacent to the stomatal opening and extending onto the inner periclinal walls. This thickening makes the stomatal slit particularly prominent in both the light microscope (Figs. 10E; 11E) and the SEM (Figs. 10F; 11D, H). The guard cells are sunken beneath, and overlapped by, usually 6 subsidiary cells with thickened inner anticlinal walls (Fig. 11E) forming the rim of the stomatal pit which might or might not bear overhanging papillae.

The upper cuticle of the leaf in Fig. 10 shows the slightly elongate ordinary epidermal cells arranged in longitudinal rows (Fig. 10A, B). The outer surface is generally smooth, but small patches of longitudinal ridges are seen on some specimens (Fig. 10C). The stomata are scattered and mostly longitudinally orientated (Figs 8G; 10A, B). The stomatal pits are typically more slit-like (Fig. 10D) than the stomata of the lower cuticle (Fig. 10E, F) but are otherwise similar, sometimes with papillae developed around the pit rim (Fig. 10A).

The lower cuticle (Fig. 11A–H) shows more isodiametric ordinary epidermal cells with tracts of slightly elongate cells, probably over the veins, arranged in longitudinal files (Fig. 11A, C). The relatively smooth outer surface is seen in Fig. 11B with the pits of the scattered and randomly orientated stomata (Figs 8H; 11A, C) more or less level with the surface. The oval pit rims bear varying numbers of subsidiary cell papillae overhanging the pit. In some stomata each subsidiary cell is papillate (Fig. 11F), others have one or two subsidiary cell papillae (Fig. 11E) and in some stomata this feature is scarcely developed at all (Fig. 11G).

The presence of numerous round and occasionally spindle-shaped resin bodies in both leaf and petiole specimens is revealed by maceration (Figs 7A, C, G; 9B). Isolated pieces of amber are also quite common in many of the debris beds processed during this study and further studies of these and other Wealden resins are underway using organic geochemical methods (Gize, pers. comm. 2000).

A female reproductive structure discovered adhering to the cuticle of a leaf segment of *G. weatherwaxiae*, and possibly attributable to it, is discussed and described below.

COMPARISON.   A single comparison of all the three species of *Ginkgoites* found in the English Wealden, and described in the present work, is given below, together with comments on species of *Ginkgoites* from Lower Cretaceous floras elsewhere.

Ginkgoites nannyoggiae sp. nov.   Figs 12–15

DIAGNOSIS.   [based on leaf fragments only] Lobes of deeply divided lamina up to at least 10 mm wide and 20 mm long with rounded apices. Circular resin bodies frequent, up to 3 per mm², 100–200 μm in diameter. Veins parallel and dichotomising, 250–600 μm apart, up to at least 12 per leaf segment.

Cuticle of both surfaces very thick; anticlinal cell walls straight; anticlinal and periclinal walls often strongly pitted. Upper cuticle usually lacking stomata, rarely with 1 per 2 or 3 mm², stomatal apparatus as for lower cuticle except indistinct and papillae absent. Ordinary epidermal cells polygonal, 4–5 sided, isodiametric,

occasionally arranged in longitudinal files, average cell-size 25 (10–40) μm. Trichomes and papillae absent.

Lower cuticle with scattered stomata usually avoiding veins; average density 69 per mm², randomly orientated. Stomatal apparatus elliptical in outline, typically 75 (44–125) μm long and 64 (44–84) μm wide; guard cells with narrow dorsal plates slightly sunken beneath ring of 4–7, usually 6, subsidiary cells each with hollow papilla overhanging oval stomatal pit. Ordinary epidermal cells of lower surface polygonal, 4–5 sided, averaging 28 (10–57) μm long and 23 (14–37) μm wide, randomly arranged or in longitudinal files; anticlinal walls straight; outer ordinary epidermal cells each with bulging outer periclinal wall bearing a large, hollow papilla.

NAME.   After Nanny Ogg, matriarch and witch of Lancre in the Discworld novels of Terry Pratchett.

HOLOTYPE AND TYPE LOCALITY.   V.64545, Fig. 12C, a dispersed leaf fragment from Galley Hill, East Sussex, locality 51 BH of Oldham (1976). Ashdown Beds Formation; Berriasian.

MATERIAL AND OCCURRENCE.   Specimens of *Ginkgoites nannyoggiae* sp. nov. have been found only as dispersed fragments, with good cuticle preservation, within the plant debris beds of the English Wealden. Although the holotype was contained in a sample collected by Oldham (1976) from the Sussex Wealden, most of the material has been found in the younger beds of the Wessex Formation in Dorset, at Worbarrow Bay and Mupe Bay. Figs 12A, B, G; 15A, E show material from Worbarrow Bay. Figs 12D–F; 14D; 15B, D show material from Mupe Bay. Figs 12C; 13A–C; 14A–C; 15C, F show the holotype from Galley Hill, East Sussex. Stratigraphical range: Berriasian – Hauterivian.

DESCRIPTION AND DISCUSSION.   The largest leaf fragments recognized so far show that *Ginkgoites nannyoggiae* sp. nov. had segments up to at least 10 mm wide with rounded apices (Fig. 12A–C). At present there is no evidence on which a whole leaf can be reconstructed nor is it known whether the leaf was petiolate. Numerous resin bodies are a prominent feature of this species throughout all the known leaf segments (Fig. 12C, G). They are revealed by maceration but the flattened discs of resin are loosened in the process and they easily dissipate with subsequent handling of the leaf.

The upper cuticle of *G. nannyoggiae* (Figs 12E–G; 13B; 14A–C) shows isodiametric ordinary epidermal cells arranged either randomly (Fig. 12G) or in longitudinal files (Fig. 12F). Figs 12G and 14B show the heavily pitted appearance of both the anticlinal and periclinal walls. An interesting feature of the outermost surface of the upper cuticle is the presence, on some specimens, of sparsely scattered oval scars. In the light microscope these scars can be seen to overlap 2–3 ordinary epidermal cells (Fig. 14A) and the SEM reveals them to be simple rimmed depressions (Fig. 14C). It seems most likely that they are the bases of thinly cutinized trichomes which were either shed in life or subsequently lost during fragmentation of the leaf. The adaxial outer surface is otherwise rather smooth and featureless (Fig. 12E).

The cuticle of the lower surface (Figs 12D; 13A, C; 14D; 15A–F)

Fig. 11 A–H   *Ginkgoites weatherwaxiae* sp. nov. All cuticle of lower surface of leaf. **A,** stomatal distribution and arrangement of ordinary epidermal cells, V.64539, LM, × 125; **B,** relatively smooth outer surface of cuticle showing stomatal pits level with general surface, V.64542, SEM, × 125; **C,** inner surface of cuticle showing scattered stomata, V.64542, SEM, × 125; **D,** 3 stomata viewed from inside, showing variable orientation V.64542, SEM, × 500; **E,** single stoma with prominent stomatal slit, thickening around pit rim, thickening extending along radial anticlinal walls of the subsidiary cells and papillae overhanging stomatal pit, V.64539, LM, × 500; **F,** highly papillate stoma viewed from outside, one large papilla on each subsidiary cell, V.64532, SEM, × 750; **G,** non-papillate stoma viewed from outside showing upper surface of guard cells and stomatal slit, V.64542, SEM, × 750; **H,** single stoma viewed from inside showing guard cells with thickly cutinized semi-circular dorsal plates and thickened inner anticlinal walls, V.64542, SEM, × 750.
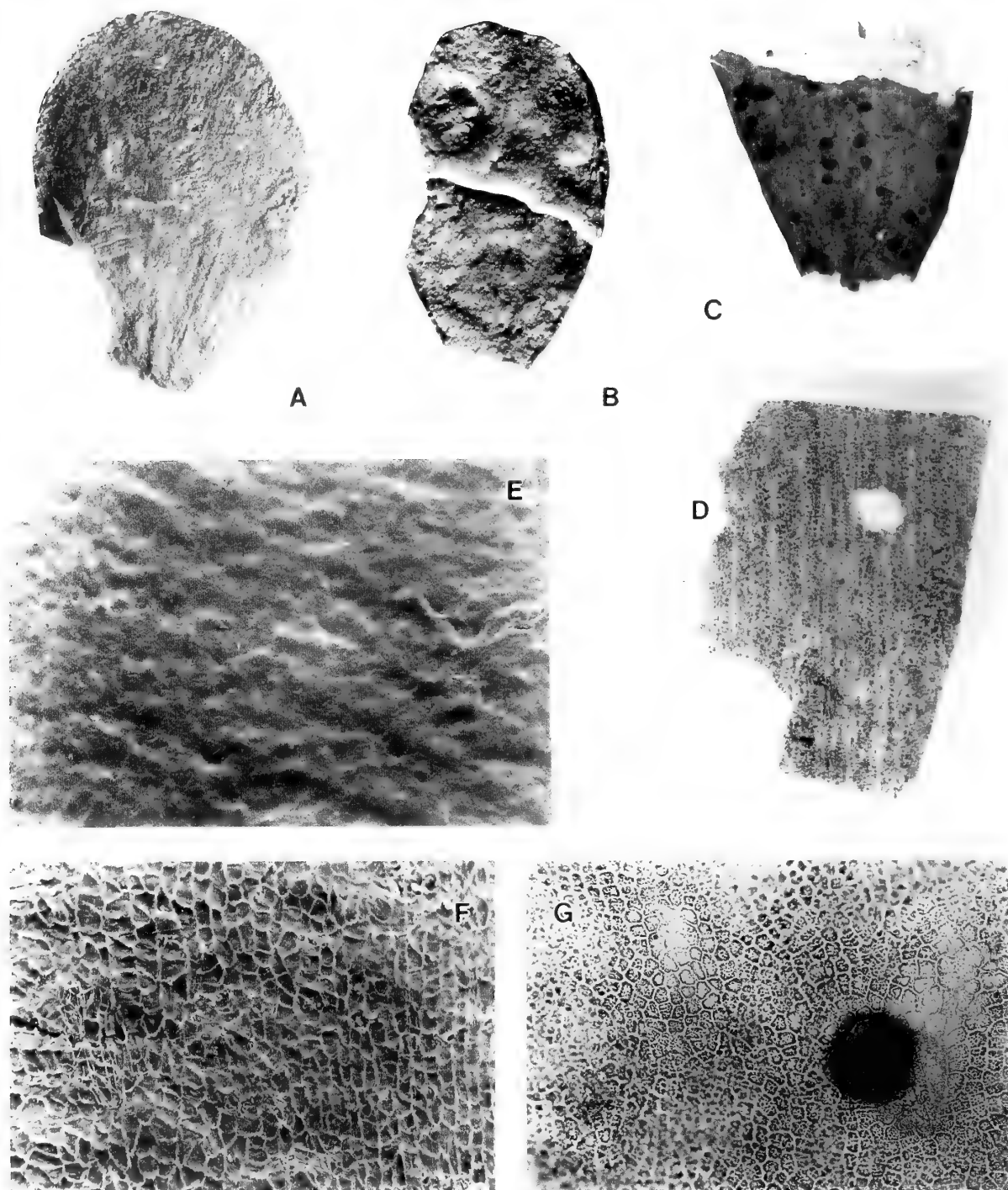
Fig. 12 A–G *Ginkgoites nannyoggiae* sp. nov. **A, B, G** from Wessex Formation, Worbarrow Bay, Dorset. **D–F** from Wessex Formation, Mupe Bay, Dorset. **C** from the Fairlight Clays facies of Ashdown Beds, Galley Hill, Sussex. **A,** largest leaf segment known, showing a hint of vein courses in lower part, V.64543, × 4; **B,** broken leaf segment, V.64544, × 4; **C, holotype**; lower part of leaf segment with numerous resin bodies, V.64545, LM, × 10; **D,** lower cuticle with large bite mark, V.64546, LM, × 20; **E,** outer surface of upper cuticle, V.64546, SEM, × 125; **F,** inner surface of upper cuticle, showing ordinary epidermal cells arranged in vague longitudinal files, V.64546, SEM, × 125; **G,** upper cuticle showing randomly arranged ordinary epidermal cells and large circular resin body, V.64547, LM, × 125.
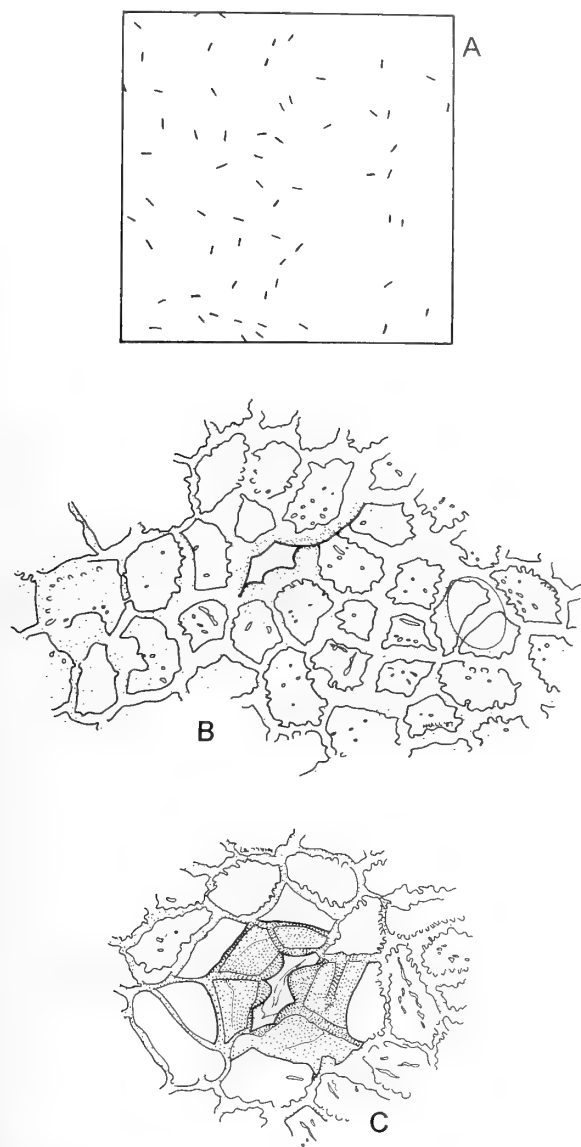
Fig. 13 A–C *Ginkgoites nannyoggiae* sp. nov. All show holotype, V.64545, from Fairlight Clays of the Ashdown Beds, Galley Hill, Sussex. **A,** stomatal distribution for lower cuticle, × 50; **B,** upper cuticle showing pitting of anticlinal and outer periclinal walls of epidermal cells, a stoma (left hand side) with ill-defined subsidiary cells and an oval scar overlying two epidermal cells, × 400; **C,** a single stoma on the lower cuticle; inner periclinal cutinization of subsidiary cells and part of an encircling cell (right hand side) giving darker appearance; outline of guard-cell dorsal plates unclear in places, × 400.

contrasts greatly with that of the upper surface. It bears numerous scattered stomata and has a densely papillate surface (Figs 12D; 14D; 15A, B). The ordinary epidermal cells, which bear the same pitting seen in the upper cuticle (Fig. 15F), are isodiametric (Fig. 15C) or longitudinally elongate and randomly arranged (Fig. 15A), or in vague longitudinal files (Fig. 14D). The bulging outer surface of each cell bears a large, prominent, hollow papilla (Fig. 15A, B). Although veins are not clearly detectable on the leaf surface, vein courses are indicated on the lower cuticle by the absence of stomata

and less pronounced papillae in some specimens (Fig. 12D). There is not enough information to indicate venation for a whole segment width but the specimen in Fig. 12D shows at least 12 veins. Fig. 15D shows the typical surface appearance of the stomatal apparatus forming a smooth flat area between the surrounding papillate cells. The papillae on the subsidiary cells are smaller, flattened and protrude over the oval stomatal pit. Fig. 15E shows two stomata in which the subsidiary cell papillae are larger and give an appearance similar to that of the ordinary epidermal cells. The 6 or so subsidiary cells of each stoma are less pitted than the ordinary epidermal cells (Fig. 15F). The guard cells tend to be obscured in the light microscope by the strong papillation of the other cells but an inner view in the SEM (Fig. 15F) shows them to have narrow dorsal plates which bear fine radiating striae on the inside. This stoma appears to have true encircling cells adjacent to the two subsidiary cells on the right hand side, and encircling cells are also shown in the stoma in Fig. 13C.

The fragment of lower surface cuticle in Figs 12D, 14D shows what is thought to be post-mortem arthropod damage: there is no reaction tissue around the edge of the regular circular hole.

COMPARISON.   See below for a comparison of all the three species of *Ginkgoites* known to occur in the English Wealden and formally described here for the first time. Comparisons with similar species in Lower Cretaceous floras from elsewhere are also made.

Ginkgoites garlickianus sp. nov.   Figs 16–19

1976   26 Gink GiA Oldham (Code used instead of Linnean binomial): 460; pl. 69, figs 1–6.

DIAGNOSIS.   [based on leaf fragments only; leaf probably deeply divided and petiolate] Ultimate lobes up to 3 mm wide and at least 4 mm long [apices unknown]. Stomata scattered on both leaf surfaces, cuticle 6 µm thick. Stomatal apparatus more or less round to elliptical; guard cells with thickly cutinized semi-circular dorsal plates and inner anticlinal walls, polar areas thinner; sunken beneath ring of 4–7, usually 5, thickly cutinized subsidiary cells forming stomatal pit. Ordinary epidermal cells less thickly cutinized than subsidiary cells, polygonal, mainly 4-sided; anticlinal walls straight.

Stomata of upper surface about 41 per mm², avoiding vein tracts; stomatal apparatus 69 (57–81) µm long and 57 (44–77) µm wide; pit oval or slit-like; aperture usually longitudinally orientated. Subsidiary cells have a hollow papilla overhanging guard cells. Ordinary epidermal cells isodiametric or longitudinally elongate, averaging 44 (20–78) µm long and 20 (10–37) µm wide; some cells at segment margins with flat outer surface. Most cells with more than one papilla or trichome, up to 50 µm long, many papillae joining to give ridge-like thickenings to surface.

Stomata of lower surface 83 (58–93) per mm²; stomatal apparatus 65 (40–108) µm long and 58 (37–108) µm wide; pit round or square, subsidiary cells sometimes possessing small papillae which overhang pit; apertures randomly or longitudinally orientated. Ordinary epidermal cells averaging 31 (10–54) µm long and 28 (10–54) µm wide, isodiametric or longitudinally elongate at segment margins where they are arranged in longitudinal files; outer surface flat, lacking thickenings and papillae.

NAME.   After Magrat Garlick, witch and Queen of Lancre in the Discworld novels of Terry Pratchett.

HOLOTYPE AND TYPE LOCALITY.   V.64548, Fig. 16A, a dispersed leaf fragment from the 'Grange Chine Black Band' plant debris bed at Grange Chine on the South West coast of the Isle of Wight (Locality L11 of Stewart 1978). Wessex Formation; Barremian.

MATERIAL AND OCCURRENCE.   All the specimens of *Ginkgoites*
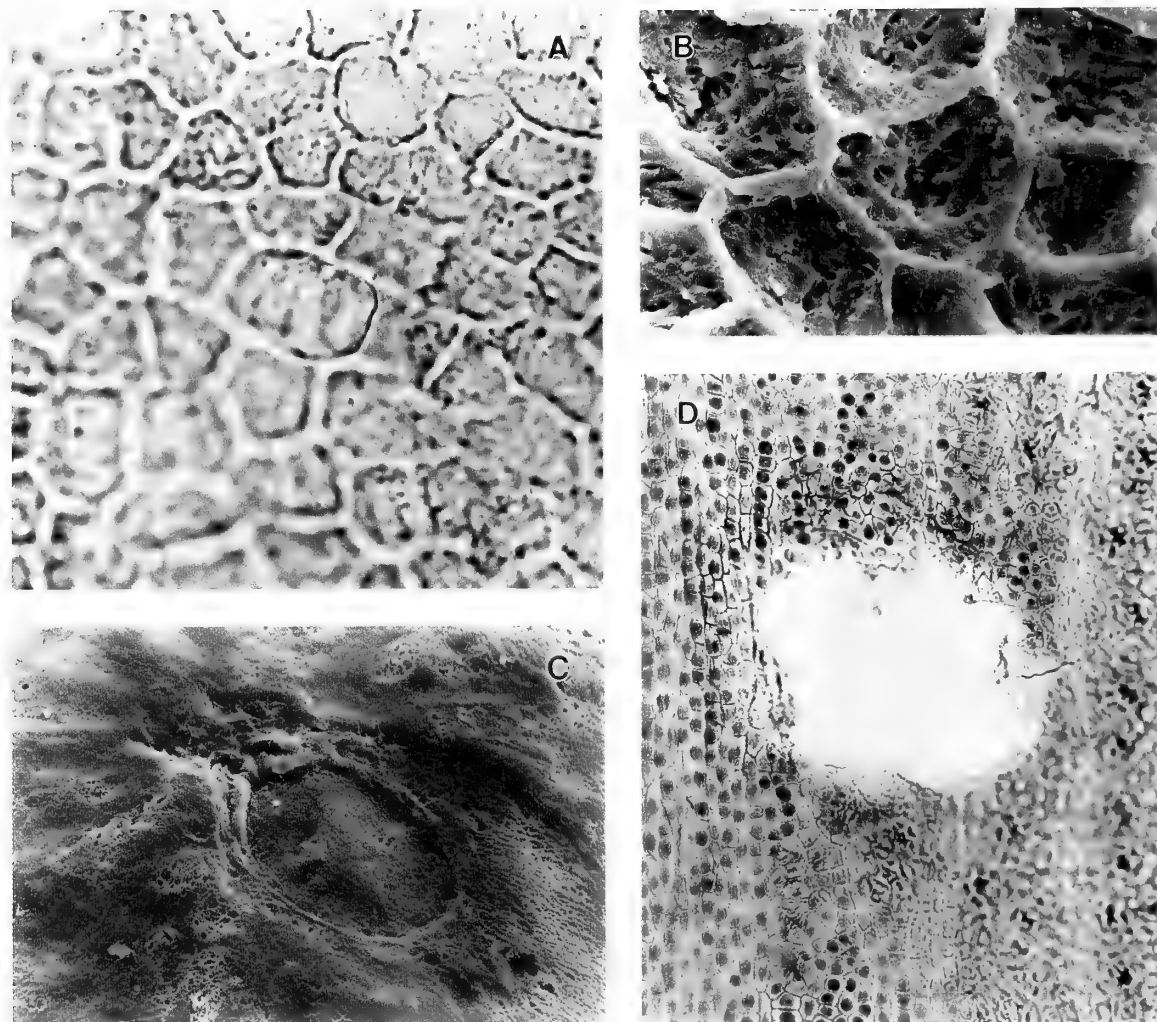
Fig. 14 A–D   *Ginkgoites nannyoggiae* sp. nov. A–C show the holotype from Fairlight Clays facies of Ashdown Beds, Galley Hill, Sussex. D from Wessex
Formation, Mupe Bay, Dorset. **A,** upper cuticle showing oval scar overlapping 3 ordinary epidermal cells, V.64545, LM, × 500; **B,** inside of upper cuticle
showing pitting, V.64545, SEM, × 1000; **C,** oval scar on outside of upper cuticle, V.64545, SEM, × 750; **D,** possible post-mortem bite-mark, V.64546,
LM, × 100.

garlickianus sp. nov. figured here have been found as dispersed
fragments with good cuticle preservation in the 'Grange Chine Black
Band' plant debris bed at Grange Chine on the South West coast of
the Isle of Wight (Locality L11 of Stewart 1978). This bed, as
previously discussed, is an important source of vertebrate material
(see introduction). Oldham (1976) described and figured material
belonging to this species from various Wessex Formation localities
along the South West coast of the Isle of Wight. Stratigraphical
range: Barremian.

DESCRIPTION AND DISCUSSION.   *Ginkgoites garlickianus* sp. nov. is
one of three species from the English Wealden newly described in
the present work and attributed to the genus *Ginkgoites* Seward.
Although Oldham (1976) recognized the cuticle of *G. garlickianus*
as of ginkgoalean affinity, he did not place it within a genus or erect
a species for it, using instead the Biorecords code 26 Gink GiA.
   The few leaf fragments of *G. garlickianus* recognized so far
indicate a lamina which is deeply divided into narrow segments and
Fig. 16A shows a leaf segment with its complete width intact.

However, no conclusive evidence from a petiole or branching or leaf
apices of segments, which would establish a gross morphology for
the leaf of this species, has yet been recognised.
   The cuticle of the upper epidermis (Figs 16C–G; 17B; 18A–C) is
covered by numerous, prominent papillae and trichomes on its outer
surface (Figs 16B, C) and is thus easily distinguished from that of the
lower epidermis (Figs 16B; 19A–F) which has a smooth and feature-
less outer surface (Fig. 19B). The upper cuticle shows the ordinary
epidermal cells arranged in longitudinal files (Fig. 16C, E); this
combines with the papillate nature of the cells to provide a ridged
structure to many areas of cuticle (Fig. 16D, F). The trichomes,
which are up to 50 µm long, are often flattened (Fig. 16E) and only
broken bases remain in some cases. The stomata are randomly
arranged and usually longitudinally orientated (Figs 16E; 17B, 18A–
C), and are similar to those of the lower surface. Although easily
recognised in the SEM, stomata are less easy to identify in the light
microscope, especially at low magnifications.
   The ordinary epidermal cells of the lower cuticle are mostly
isodiametric and randomly arranged (Figs 19A, C); the outer surface
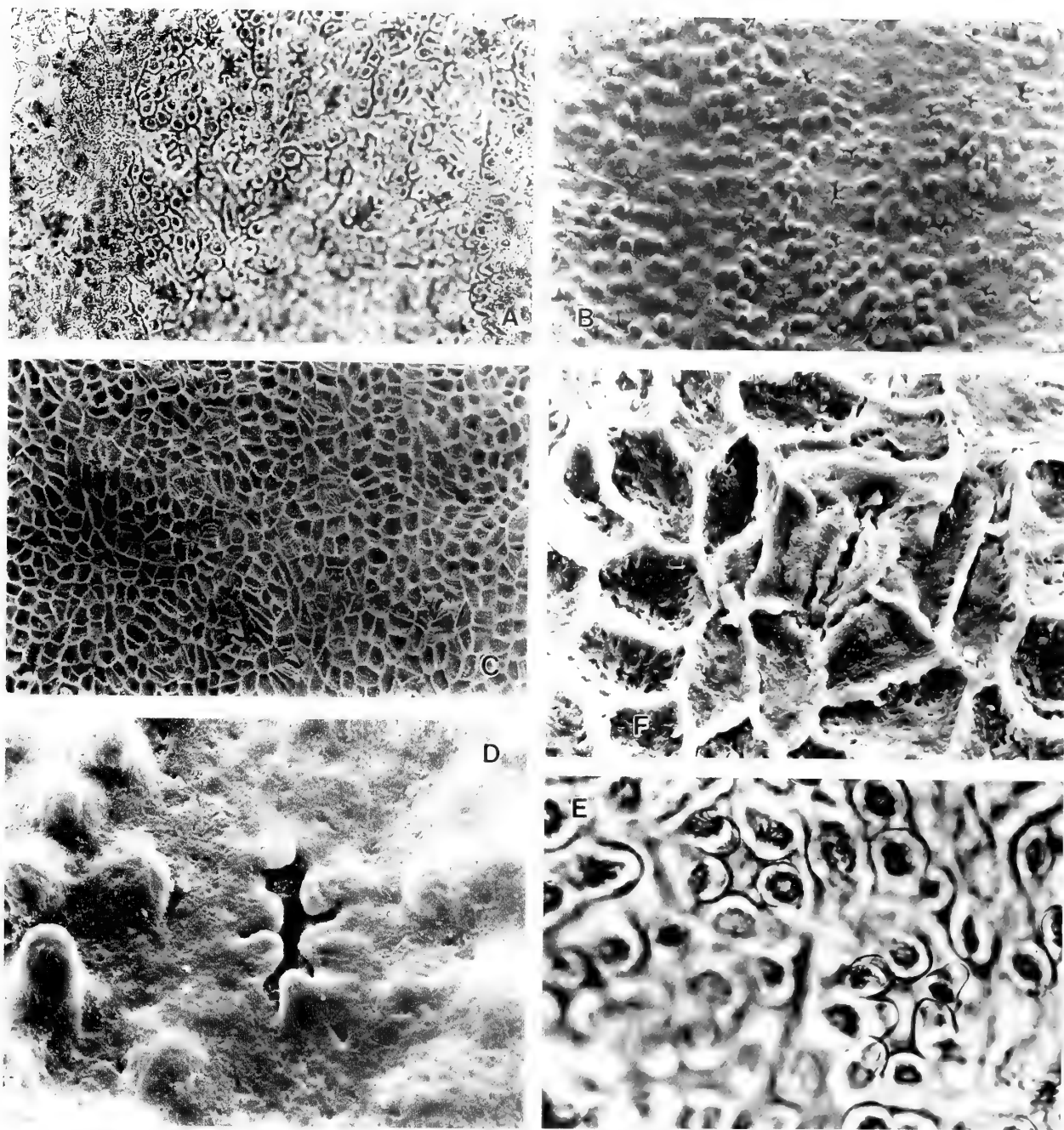
Fig. 15 A–F *Ginkgoites nannyoggiae* sp. nov. **A, E** from Wessex Formation, Worbarrow Bay, Dorset. **B, D** from Wessex Formation, Mupe Bay, Dorset. **C, F** show the holotype, from Fairlight Clays facies of Ashdown Beds, Galley Hill, Sussex; all lower cuticle. **A,** random arrangement of papillate ordinary epidermal cells, V.64547, LM, × 125; **B,** outer surface of cuticle showing stomatal distribution and papillate surface, V.64546, SEM, × 125; **C,** inner surface of cuticle showing randomly arranged polygonal, isodiametric ordinary epidermal cells and scattered stomata, V.64545, SEM, × 125; **D,** outside of single stoma showing small, flattened papillae overhanging pit, V.64546, SEM, × 750; **E,** 2 stomata with large protruding papillae, V.64547, LM, × 500; **F,** single stoma viewed from inside showing narrow dorsal plates of guard cells which bear fine radiating striae, V.64545, SEM, × 750.

is smooth and featureless (Fig. 19B). Fig. 19C shows the stomata scattered and randomly orientated. The guard cells, with well cutinized 'axe-head-shaped' dorsal plates and inner anticlinal walls (Fig. 19F), are sunken beneath a ring of typically 5 subsidiary cells, and are sometimes partially exposed (Fig. 19D). The subsidiary cells sometimes bear flat papillae which overhang the round or square stomatal pit (Fig. 19E); others have a simple rim (Fig. 19D). This is a character that varies a great deal between specimens but is fairly constant for any particular specimen. Clearly further finds, particularly less fragmentary portions of leaf, are needed to enhance our
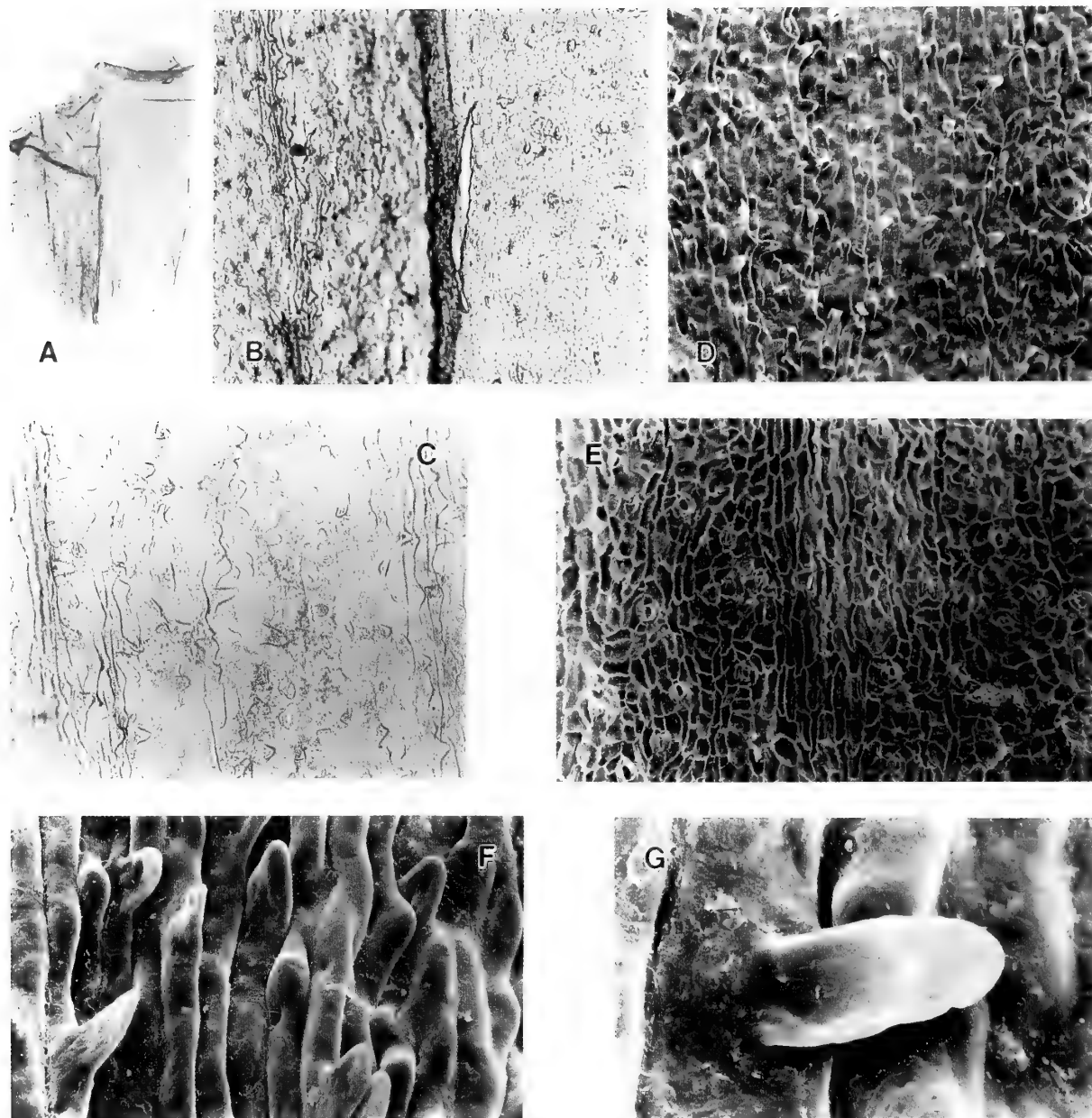
Fig. 16 A–G   *Ginkgoites garlickianus* sp. nov. **A, holotype**; leaf fragment showing full segment width, V.64548, LM, × 10; **B**, segment margin of holotype, dividing upper (left) and lower (right) cuticle, V.64548, LM, × 75; **C–G** upper cuticle; **C,** heavily papillate cuticle, showing large ridge on left, V.64548, LM, × 125; **D,** outer surface of cuticle showing whole and broken papillae, V.64549, SEM, × 125; **E,** inside of cuticle showing ordinary epidermal cells in rows and stomatal distribution, V.64548, SEM, × 125; **F,** ridged outer surface bearing flattened papillae and possible stomatal opening (bottom right), V.64549, SEM, × 500; **G,** single flattened papilla, V.64549, SEM, × 1000.

knowledge of this species. This is a distinct possibility since its distinctive suite of characters makes for fairly easy recognition, but it requires further intensive searching of debris material.

COMPARISON.   Of the 3 species of *Ginkgoites* present in the English Wealden, the most easily distinguished is *Ginkgoites nannyoggiae* which has much the widest leaf segments, stomata confined to the densely papillate lower surface, and an upper cuticle which shows isodiametric cells only. Both *Ginkgoites garlickianus* and *Ginkgoites weatherwaxiae* have narrow segments, stomata on both surfaces and

an upper cuticle with more elongate ordinary epidermal cells than the lower. However, *G. garlickianus* has a heavily papillate, ridged upper cuticle, whereas that of *G. weatherwaxiae* is generally smooth. The stomata of the lower surface of *G. weatherwaxiae* are oval in outline and typically have 6 papillate subsidiary cells. Those of *G. garlickianus* are more circular in outline with a smaller opening and typically have 5 subsidiary cells on which the presence of papillae varies considerably between specimens. The cuticle of *G. weatherwaxiae* is in some ways more similar to that of *Czekanowskia anguae* which is also present in the plant debris beds of Worbarrow
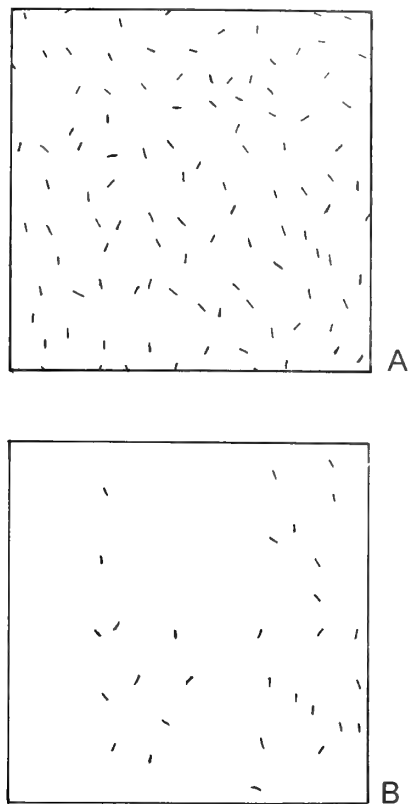
Fig. 17 A–B *Ginkgoites garlickianus* sp. nov. **A,** distribution and orientation of stomata on lower surface; **B,** distribution and orientation of stomata on upper surface; both from **holotype**, V.64548, × 50.

Bay. However, the stomata of *C. anguae* are strictly longitudinally orientated on both surfaces, are arranged in files rather than scattered, are never papillate and have 2 distinct polar subsidiary cells.

Amongst Lower Cretaceous floras from elsewhere the two species *Ginkgoites brauniana* (Dunker) from the Lower Cretaceous of Germany (Watson *et al* 1999) and *Ginkgoites pluripartita* (Schimper), a species widely distributed in the northern hemisphere (Watson *et al* 1999), show similarities to the English species. The narrow, dichotomizing segments of *G. weatherwaxiae* are similar to those seen in some specimens of *G. brauniana,* which differs however in having stomata confined to the lower surface and has lower ordinary epidermal cells bearing small median papillae. The less divided leaves of *G. pluripartita* bear a resemblance to the wide leaf segments of *G. nannyoggiae,* but *G. nannyoggiae* lacks the conspicuous venation of *G. pluripartita* and the two differ in cuticular details such as the appearance of the stomata.

Ovule attributed to *Ginkgoites weatherwaxiae*

Figs 20, 21

DESCRIPTION   Compressed oval cuticular structure, 0.7 mm long and 0.4 mm wide, comprising an inner layer composed of the megaspore membrane and associated cutinized gametophytic tissue, surrounded by the nucellar cuticle with gap of up to 40 μm between the two. Inner layer thickly cutinized with vesicles 1.3–5.4 μm in diameter irregularly scattered throughout; aggregations of vesicles often in centre of ill-defined polygonal cells about 60 μm across.
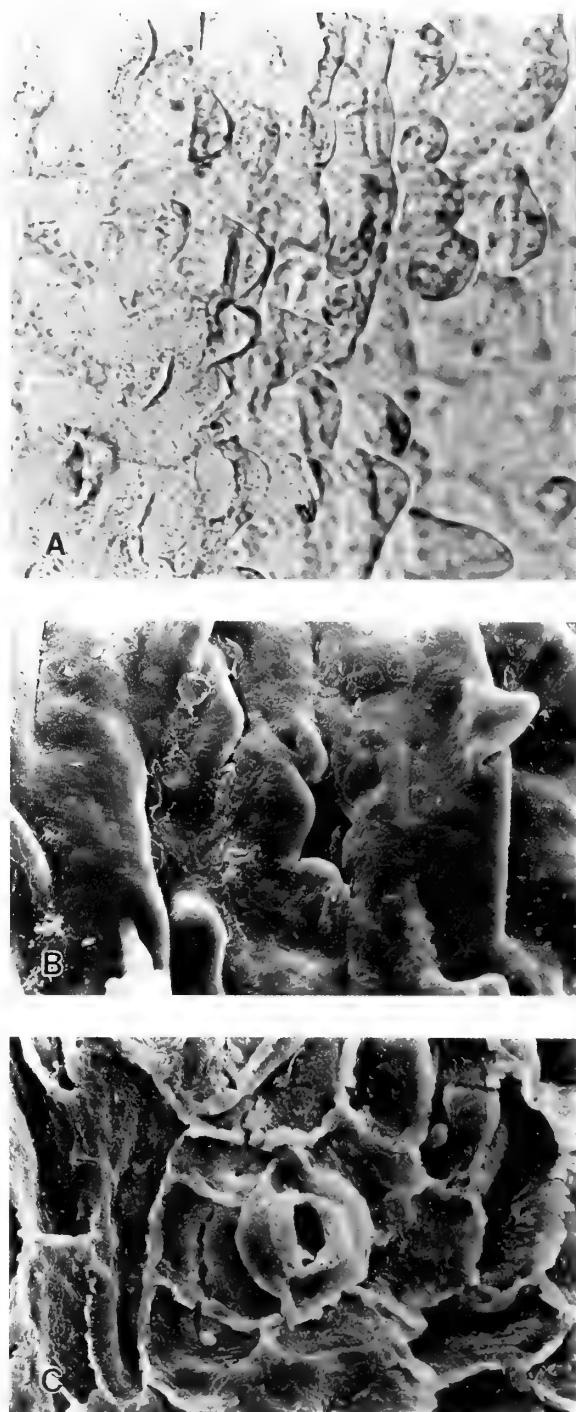
Fig. 18 A–C   *Ginkgoites garlickianus* sp. nov. All upper cuticle. **A, holotype,** single stoma obscured by subsidiary cell papillae, V.64548, LM, × 500; **B,** papillate stomatal pit viewed from outside, V.64549, SEM, × 750; **C, holotype,** inner surface of upper cuticle showing single stoma, V.64548, SEM, × 750.

Nucellar cuticle thin, 80 μm wide at chalaza; mucronate apex or beak extending 80 μm above inner layer, forming pollen chamber. Cells straight-walled with smooth outer periclinal walls, around 100
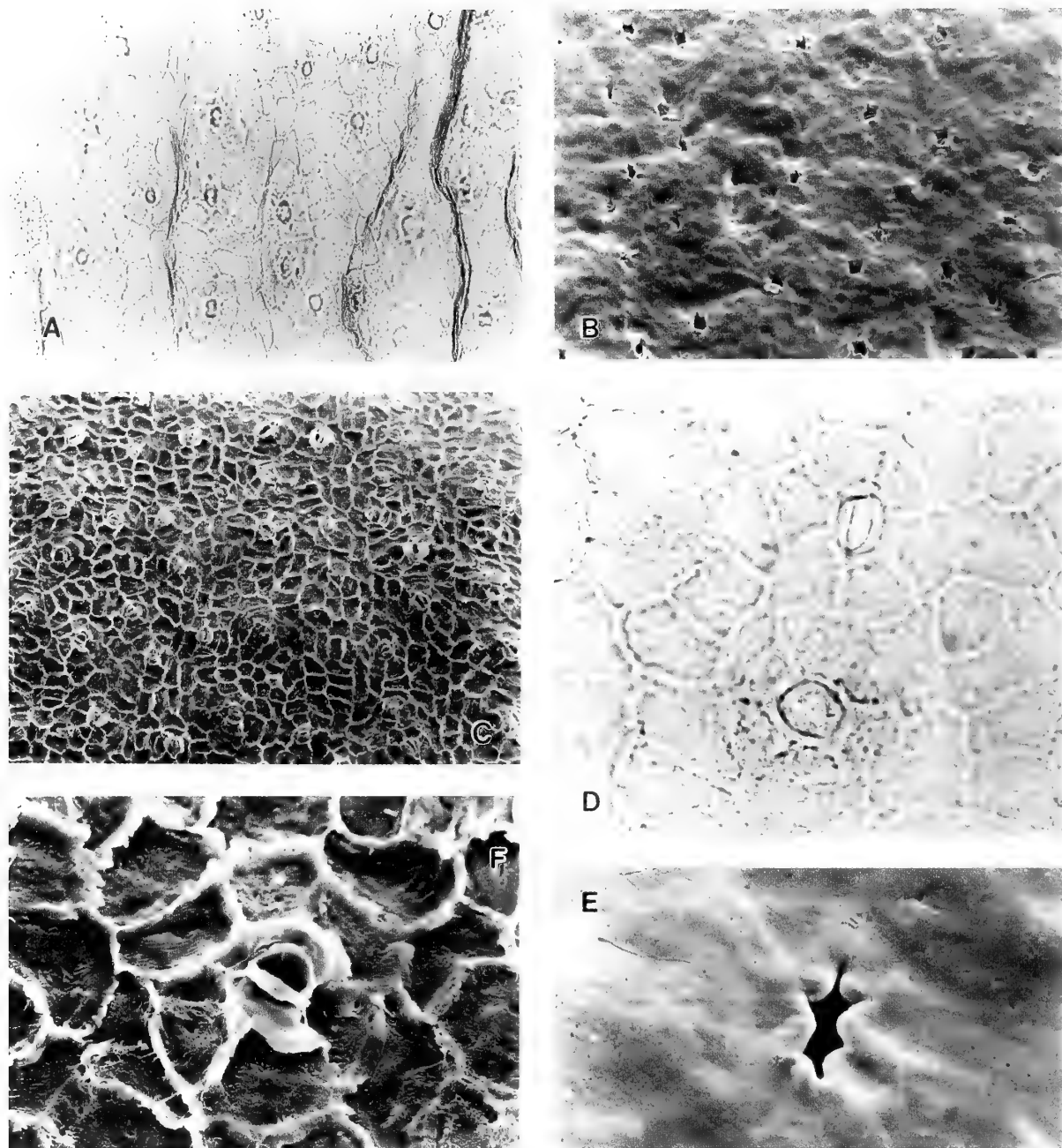
Fig. 19 A–F   *Ginkgoites garlickianus* sp. nov. All lower cuticle. **A,** isodiametric ordinary epidermal cells and scattered stomata, V.64550, LM, × 125; **B,** smooth outer surface of cuticle, V.64548, SEM, × 125; **C,** inside of cuticle showing stomatal distribution, holotype, V.64548, SEM, × 125; **D,** 2 stomata showing circular outline and thickened rim, V.64551, LM, × 500; **E, holotype,** outer surface of cuticle showing single stoma with flattened subsidiary cell papillae, V.64548, SEM, × 750; **F, holotype,** stoma viewed from inside, showing thickly cutinized semi-circular dorsal plates and inner anticlinal walls, V.64548, SEM, × 750.

µm long and 70 µm wide at chalazal end, 85 µm long and 30 µm wide near beak.

Pollen grains present within pollen chamber, elliptical, 50 µm long, monocolpate.

MATERIAL AND OCCURRENCE.   V.64552, Fig. 20A–C, a compressed ovule retrieved following maceration of an isolated leaf fragment of *Ginkgoites weatherwaxiae*, is the only specimen to have been found at present. It is from the plant debris beds of Worbarrow Bay, Dorset.

Wessex Formation; Hauterivian.

DISCUSSION.   Interpretation of this structure, the only reproductive body to have been associated with ginkgoalean material from the English Wealden to date, is difficult, particularly as there is only a single compressed specimen (Figs 20A–G; 21) available for study. However, the general morphology (Fig. 20A–C) is clearly that of an orthotropous gymnosperm ovule.

The ovule was found in so close an association with a leaf
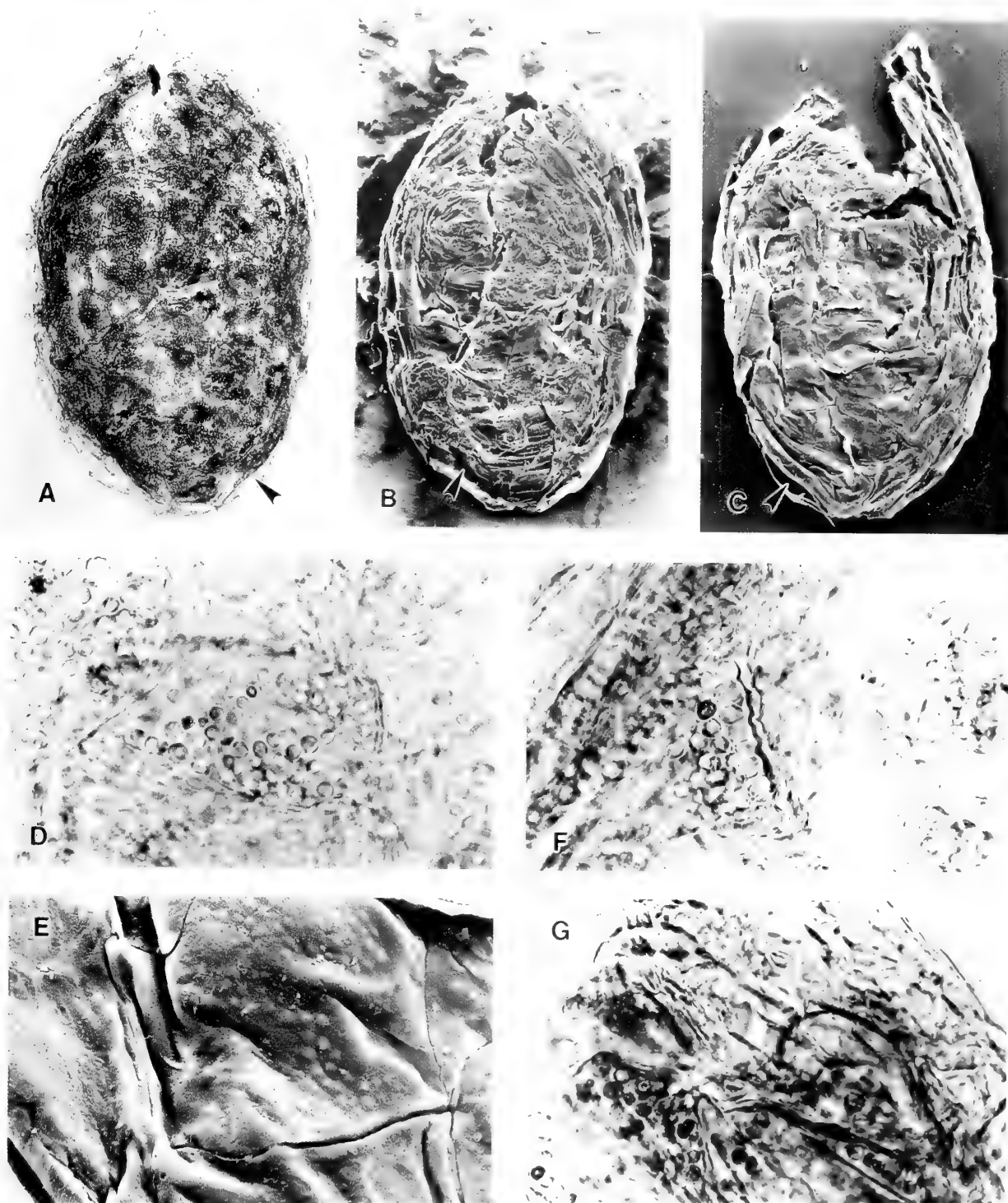
Fig. 20 A–G   Ovule attributed to *Ginkgoites weatherwaxiae* sp. nov. V.64552. **A,** ovule seen in the light microscope, showing general morphology and two layers of cuticle; arrow indicates gap between them; LM, × 125; **B,** ovule mounted on a stub with same side uppermost as for LM in A; outer cuticle present over most of the surface; where absent, showing well-defined wall dividing inner cuticle, SEM, × 125; **C,** ovule remounted to show reverse side; outer cuticle present only at margins, inner cuticle showing polygonal cells divided by cracks; arrow indicates gap between them; SEM, × 125; **D,** inner cuticle showing aggregation of vesicles in centre of cell, LM, × 750; **E,** inner cuticle showing cracks defining cell margins and raised impressions of vesicles, SEM, × 750; **F,** well-defined wall seen in middle of apical end of inner cuticle, LM, × 750; **G,** two pollen grains found in outer cuticle in apical region, LM, × 750.

Fig. 21   Ovule attributed to *Ginkgoites weatherwaxiae* sp. nov., V.64552. Wessex Formation, Worbarrow Bay, Dorset. Apex showing vesicles and distinct longitudinal wall in megaspore membrane cuticle, cell walls of nucellar cuticle and two pollen grains lodged within pollen chamber; × 375.

fragment of *Ginkgoites weatherwaxiae* that its presence was not detected until revealed by maceration. We have decided to attribute it to this species as no features of the ovule are in disagreement with this interpretation. Unfortunately, there are no cuticular characters that can be used to link this structure to this, or indeed to any other, leaf species. If it does not belong to *G. weatherwaxiae*, it could potentially belong to any of the ginkgoaleans, cycads (Watson & Cusack Drury, in preparation) or numerous unidentified gymnosperms known from leaf cuticles from the English Wealden.

Fig. 20A shows the remaining two layers of cuticle present in this ovule in the light microscope. The ovule is orthotropous, and broken at the chalaza with no evidence of the funicle. The absence of integument cuticles means that there is no direct evidence of the micropyle, and we have no way of knowing if thick flesh or a stony layer existed within the integument. Unfortunately, evidence of the structure of the ovule-bearing organ is also lacking.

Following light microscopy, the ovule was first mounted whole on a stub, displaying the damaged nucellar cuticle (Fig. 20B). It was then removed and remounted to allow SEM study of the reverse surface (Fig. 20C). This process revealed the thicker inner cuticle over most of this surface, the delicate nucellar cuticle having been lost.

The nucellar cuticle completely envelops the inner cuticle and consists of cells with a smooth outer surface and straight anticlinal walls which are longitudinally aligned and decrease in size towards the micropylar end. They are best seen at the edges of the specimen (Fig. 20A) and near the apex, particularly in the SEM which shows anticlinal walls on the inner surface (Figs 20C, 21). The mucronate apex or 'beak' which extends above the gametophyte and forms the pollen chamber is typical of most gymnosperm orders (Batten & Zavattieri 1996: 710).

The inner cuticle is very thick and contains conspicuous vesicles which are often aggregated in the centre of ill-defined polygonal cells (Figs 20D, 21). In the SEM, the outer surface shows these cells to be separated by fine cracks (Fig. 20C, E) and the vesicles can also be seen to form raised impressions on the cuticle surface (Fig. 20E).

This cuticle has a distinctive wall, associated with a crack in the nucellar cuticle, running longitudinally down the middle from the micropylar end. This can be seen both in the light microscope (Figs 20F; 21) and in the original SEM view of the surface where a break in the outer cuticle exists (Fig. 20B). In this view it can be seen to meet with a similar wall on the right-hand side a little further down.

These distinctive features of the inner cuticle are best interpreted by comparison with the development of the female gametophyte of *Ginkgo biloba*, as described by Soma (1997). During the free nuclear division phase, the gametophyte increases in size and the megaspore membrane thickens. Cell wall formation follows, gradually proceeding in files from the periphery towards the centre. The innermost cells of the gametophyte fail to join and the opposite files of cells form two distinct abutting walls, so that a mature female gametophyte can be split easily in two. The tissues of the mature female gametophyte show a high degree of cell differentiation. The very outermost cells are filled with lipid droplets and surround cells bearing protein lipid and starch reserves (Rohr 1997; Soma 1997).

In most ginkgoaleans the megaspore membrane is granular and non-cellular (Archangelsky 1965; Zhou & Zhang 1989,1992; Zhou 1993). It seems to us that in this ovule the outer layer of the gametophyte is also cutinized, preserving its polygonal cell structure, and that this cutinized layer cannot be distinguished from the megaspore membrane. The globular vesicles seen throughout these gametophytic cells almost certainly represent lipid droplets, and the longitudinal split of the gametophytic tissue, defined by a distinct wall, may well be evidence of centripetal development in two distinct parts as in *G. biloba*. Although cutinization of the gametophyte has not been previously described in fossil ginkgoaleans, impressions of gametophytic tissue on the megaspore membrane have been recorded in the ovules of *Yimaia hallei* (Sze) Zhou et Zhang from the Middle Jurassic of Henan, China (Zhou & Zhang 1992). *Ginkgo yimaiensis* Zhou et Zhang, of the same age and provenance, also has a megaspore membrane which may bear obscure outlines of 'prothallial cells' (Zhou & Zhang, 1989: 122). A similar phenomenon was described by Harris (1943) in the Yorkshire Jurassic

conifer *Elatides williamsoni* Harris. In this species, the megaspore membrane is combined with what Harris called the 'outer cell-layer of the endosperm' (Harris 1943: 332). This consists of large, brown, straight-walled isodiametric cells, occasionally incompletely filled and represented by more or less isolated globular masses. Harris interpreted these as the oily food reserves of the prothallus which have been converted into a resistant mass of resin (Harris 1943, 1954). It is evident that a fairly unusual mode of preservation has occurred and that more specimens will need to be found and studied in order to improve our understanding of this structure.

Two pollen grains can be seen within the pollen chamber formed by the nucellar beak (Figs 20G; 21) using the light microscope, although they are obscured by both cuticular layers. A median colpus can be recognised on one of the pair (Fig. 21). Monocolpate pollen has been found within, and closely associated with, other fossil ginkgoalean ovules (Krassilov 1972; Harris & Millington 1974; Zhou & Zhang 1989, 1992), but it is associated with various gymnosperm groups, including the Ginkgoales, Cycadales and Bennettitales (Batten 1974) and any speculations as to affinity, based on two partially obscured grains of pollen from a single ovule are, at best, inconclusive.

COMPARISON. The ovule attributed to *Ginkgoites weatherwaxiae* can be compared to previously described ginkgoalean female reproductive structures. Zhou (1997) presented a review of Mesozoic ginkgoalean genera, of which *Allicospermum* Harris, *Karkenia* Archangelsky, *Yimaia* Zhou et Zhang and fossils referred to *Ginkgo* L. are of relevance here. All of these share the same basic structure: an orthotropous ovule with a thick megaspore membrane, a thin nucellar cuticle and an integument, with an inner and an outer cuticle, showing well-developed fleshy and stony layers.

Allicospermum is a form-genus of broad scope which may well include seeds of various plant groups, including the Ginkgoales, Cycadales and Coniferales. Several species are believed to be the seeds of fossil ginkgoaleans, including the type species, *A. xystum* Harris, from the Lower Jurassic of East Greenland (Harris 1935), which is attributed to the leaf species *Ginkgoites taeniata* (Braun) Harris. These seeds tend to be much larger than the ovule described here. The other three genera differ in the size, number and arrangement of ovules in the ovule-bearing organ: fossils attributed to *Ginkgo* bear 2–3 large orthotropous ovules attached to a peduncle, *Yimaia* is a form-genus for clusters of sessile ovules borne on the end of a peduncle (Zhou & Zhang 1992) and the genus *Karkenia* was erected for organs bearing many small pedunculate ovules on a central axis (Archangelsky 1965). The ovules of *Ginkgo* and *Yimaia* are generally large and *Karkenia*, though considerably smaller, bears ovules about three times the size of that attributed to *G. weatherwaxiae*.

Evidence of the nature of the integument is entirely lacking, as is that of the structure of the ovule-bearing organ, and we feel it would be inappropriate to place the ovule described here within any of these genera, even though shared similarity in structure is clear.

Comparisons can also be made with *Spermatites*, a genus erected by Miner (1935) for small hollow cuticular structures from the Upper Cretaceous of Western Greenland. He was unsure as to their affinity and employed *Spermatites* 'as a convenient designation for such unassigned organs' (Miner 1935: 597), although he did recognise that they probably represented seeds. The majority of species are of late Early to Late Cretaceous age (Batten & Zavattieri 1995) and may represent the seed coats of close relatives of the extant rush genus *Juncus* (Binda & Nambudiri 1983; Batten & Zavattieri 1996). However, older species attributed to this genus appear to be of gymnospermous origin and Batten & Zavattieri suggested that it

should be regarded as a 'heterogeneous taxon that includes representatives of a variety of plant groups' (Batten & Zavattieri 1995: 77).

Spermatites pettensis Hughes, from the Ashdown Beds Formation of the English Wealden (Hughes 1961), is a seed of the same size and general morphology as the ovule described here. Cuticle described by Oldham (1976) as 29 Gink GkC and now known to be *G. weatherwaxiae* occurs in the same beds as *S. pettensis*. Hughes interpreted the structure as a gymnospermous ovule consisting of a thick, punctate nucellar cuticle forming a well developed pollen chamber, covered in its upper half by thin inner integument cuticle which continued into a long micropylar tube. He also noted the presence of *Eucommiidites* pollen in the micropylar tube and the pollen chamber. *S. pettensis* was subsequently reinterpreted by Reymanówna (1968) in accordance with her description of Polish *Eucommiidites*-containing specimens of *Allicospermum retemirum* Harris, a seed species originally described from the Middle Jurassic of Yorkshire (Harris 1944). She observed that although *A. retemirum* is about five times larger than *S. pettensis*, the cuticles present are virtually the same: a thick megaspore membrane and a nucellar cuticle with an extended micropylar tube. This interpretation of the cuticles present in *S. pettensis* indicates a much closer similarity with the ovule described here. However, the megaspore membrane of *S. pettensis* does not bear cell outlines or contain vesicles, and the nucellar cuticle, which covers only its upper half, forms a long protruding micropylar tube rather than a small beak.

The presence of *Eucommiidites* pollen in both *A. retemirum* and *S. pettensis* is of importance, as the affinities of *Eucommiidites*-bearing seeds have been suggested to lie with the Gnetales, Bennettitales and Pentoxylales (Hughes 1961; Pedersen *et al* 1989). It is not impossible that the obscured pollen grain bearing a median colpus within the ovule described here could bear two subsidiary colpi which have not been recognized. This would alter our view of the affinities of this ovule considerably, and it is clear that more material is needed in order to describe it more thoroughly.

Order **CONIFERALES**
INCERTAE SEDIS (family uncertain)
Genus *PSEUDOTORELLIA* Florin

1936a   *Pseudotorellia* Florin: 142.
1957   *Pseudotorellia* Florin; Lundblad: 760. [Florin's diagnosis translated into English]
1969   *Pseudotorellia* Florin; Watson: 248. [Diagnosis emended]
1969   *Tritaenia* Mägdefrau & Rudolf: 296.
1990   *Pseudotorellia* Florin; Bose & Manum: 49. [Diagnosis emended]
1991   *Tritaenia* Mägdefrau & Rudolf; Bose & Manum: 14.
1998   *Pseudotorellia* Florin; Watson & Harrison: 240.
2000   *Tritaenia* Mägdefrau & Rudolf; Manum, Van Konijnenburg-Van Cittert & Wilde: 257.

TYPE SPECIES. *Feildenia nordenskjoeldii* (Nathorst), 1897: 56, pl. 3, figs 16–27

DIAGNOSIS. [slight emendation by Bose & Manum (1990) of the translation by Lundblad (1957) of the original of Florin] Leaves coriaceous, entire or microscopically dentate, almost linear to narrowly tongue-shaped or obovate, straight or slightly falcate, with their maximum width in the middle region or more apically; apex obtuse; gradually narrowing towards base, hardly forming a petiole. Veins moderate in number, dichotomizing chiefly in basal part, ending separately at, or just below apical margin. Lamina with or without resin ducts.

Stomata confined to lower side in stomatal strips between narrower, non-stomatal longitudinal zones. Within strips stomata in short longitudinal rows or irregularly scattered, sparse or crowded, always longitudinally orientated. Guard cells sunken, next to the slit showing a more or less strongly cutinized ridge ('Vorhofleiste') and side wall facing lateral subsidiary cell also strongly cutinized. Subsidiary cells 4–6. Epidermal cells with slightly sinuous to straight outlines, surface of one or both sides having a median longitudinal ridge.

DESCRIPTION.   In addition to the characters in the original diagnosis above, Watson & Harrison (1998) have recognised three other distinctive features in four species attributed to the genus *Pseudotorellia* Florin. These are: a tendency for ordinary epidermal cells to occur in pairs with the common wall narrower than the other anticlinal walls (Fig. 22L); cutinization of the guard cells as narrow, elongate, thickly cutinized dorsal plates (Fig. 22H, I) and strongly developed polar appendages (Fig. 22I, N); unbranched resin canals running along the entire length of the leaf (Fig. 23E, F); all of which are coniferous characters and some at least are probably diagnostic. However, with problems both of generic usage (discussed below) and the original attribution of *Pseudotorellia* to the Ginkgoales it seems to us prudent not to embark on emending the diagnosis at this stage.

DISCUSSION.   The genus *Pseudotorellia* was erected by Florin (1936a: 142) as a form-genus to accommodate species of lanceolate, non-petiolate leaves attributed to the Ginkgoales and subsequently various authors (e.g. Lundblad 1957, Watson 1969, Krassilov 1972, Bose & Manum 1990) erected a total of ten or more species of multi-veined leaves of this type from Northern Hemisphere Jurassic and Cretaceous floras. *Pseudotorellia heterophylla* Watson (1969) from the English Wealden was diagnosed on the basis of a very small sample of leaves isolated by Watson (1964) in the first study of fragmentary plant debris from the Hastings Beds. It was immediately obvious both to Watson (1964, 1969) and Harris (pers. comm. 1963) that wide, multi-veined elliptical leaves were attributable to the genus *Pseudotorellia* yet had cuticle which was indistinguishable from that of needle leaves in the same samples. The demonstration of two veins in the needle leaves strengthened the obvious conclusion that the two leaf types represented a single heterophyllous species. This was attributed to the genus *Pseudotorellia* without hesitation but with a necessary emendment to Florin's diagnosis. At the same time a new genus, *Tritaenia* Mägdefrau & Rudolf (1969), was erected to accommodate the needle leaves of *Abietites linkii* Römer (1839), long known in great abundance from leaf-coal deposits in the Wealden of Northwest Germany. However, following World War II, the type material of the German Wealden flora, largely held in collections in East Germany, was inaccessible for many years and serious, practical comparison between English and German species was delayed until 1979 when Fisher (1981) and Watson visited the Museum für Naturkunde, East Berlin. Unrestricted access

to all surviving German specimens followed and, together with the collection of voluminous new English material, led to major new studies, including those of Fisher (1981), Sincock (1985) and Harrison (née Hall 1987). The German *Abietites/Pseudotorellia/Tritaenia linkii* material proved to have cuticle indistinguishable from that of the English *Pseudotorellia heterophylla* Watson (1969) and in combining these two species Watson & Harrison (1998) decided that the diagnosis of *Pseudotorellia* Florin, as emended by Bose & Manum (1990; see above), presented the most suitable genus. It became clear that the discoveries made, especially the obvious heterophylly, rendered the needle-leaved genus *Tritaenia* Mägdefrau & Rudolf (1969) redundant and it therefore became a synonym of *Pseudotorellia* Florin. This status of the genus *Tritaenia* has been disputed (Manum *et al.* 2000) in conjunction with a refusal to accept the identification and synonymy of the English and German material made by Watson & Harrison (1998).

Pseudotorellia was originally assigned to the Ginkgoales rather than the broad-leaved conifers because of the veins which end freely in the apical margin, but the features described above together with others such as: very thick cuticles; exclusively longitudinal alignment of stomata; longitudinal arrangement and elongation of ordinary epidermal cells; attribution to *Sulcatocladus* shoots, are all typically coniferous rather than ginkgoalean features and the two species of *Pseudotorellia* described here, seem to us more readily accommodated amongst the broad-leaved, multi-veined conifers than the Ginkgoales.

Amongst species in other floras, *Pseudotorellia angustifolia* Doludenko (see Krassilov 1972: 58) from the Mesozoic of the Bureja Basin, Siberia is known to be attached to a *Ginkgo*-like short shoot (Krassilov 1972: pl. 20, fig. 3) although associated seeds and seed-bearing structures suggest the possibility of coniferous affinity. In the absence of complete knowledge of the female reproductive organs, but with short shoots and the association of *Ginkgo*-like pollen, Krassilov (1970, 1972) attributed *P. angustifolia* to a distinct family within the Ginkgoales, suggesting that *Pseudotorellia* corresponded to a natural genus which could be attributed in its entirety to this isolated family, the Pseudotorelliaceae. However, the attribution of *P. linkii* to *Sulcatocladus* shoots points to the coniferous nature of *Pseudotorellia* from the Wealden of England and Germany. In view of the complete lack of evidence from reproductive structures, we follow the previous suggestion of Watson & Harrison (1998) that *Pseudotorellia* Florin should at present be regarded as a gymnosperm form-genus for species attributable to either the Ginkgoales or the Coniferales.

Pseudotorellia linkii (Römer) Watson & Harrison
Figs 22–23

1839   *Abies Linkii* Römer: 10, pl. 17, figs 2a–c. [Northwest Germany]
1846   *Abietites (Abies) Linkii* (Römer) Dunker: 18, pl. 9, figs 11a–d. [Northwest Germany]

Fig. 22 A–N   *Pseudotorellia linkii* (Römer) Watson & Harrison. **A,** needle leaves at natural size; left to right V.64174-V.64195; **B,** wider leaves from the English Wealden, left to right V.64196-V.64200, × 2.5; **C,** apical part of an unmacerated leaf showing five veins ending freely, V.19021b (figd Seward, 1926; text-fig.16 A ii), Lower Cretaceous, Western Greenland, × 2.5; **D,** one of the longest and most complete needle leaves with slightly constricted base and strong midline on upper surface, V.64249, × 2.5; **E,** middle part of a needle leaf with 4 veins visible, V.64202, × 10; **F,** part of leaf in Fig. 22C showing 3 of the 5 vascular strands protruding beyond the break, × 10; **G,** rare leaf apex with extreme pointed tip intact, V.64553, × 50; **H,** lower cuticle of mid-region of leaf showing 3 stomatal bands which merge distally, V.64203, × 30; **I,** lower cuticle showing prominent stomata and pustules inside the ordinary epidermal cells, V.64203, × 125; **J,** smooth outer surface of lower cuticle with four stomata visible, V.64289, × 250; **K,** strongly ridged outer surface of lower cuticle showing three stomata, V.64290, × 250; **L,** upper cuticle with epidermal cells arranged in files and pustules on the inside of the surface walls, V.64205, × 125; **M,** inside surface of upper cuticle, showing longitudinal and transverse late division pairs of cells, hypodermis developed on left hand side, V.64289, × 125; **N,** inside view of stomatal apparatus showing cutinized dorsal plates (radially striate), inner anticlinal walls, part of the ventral walls and polar appendages, V.64289, × 500.
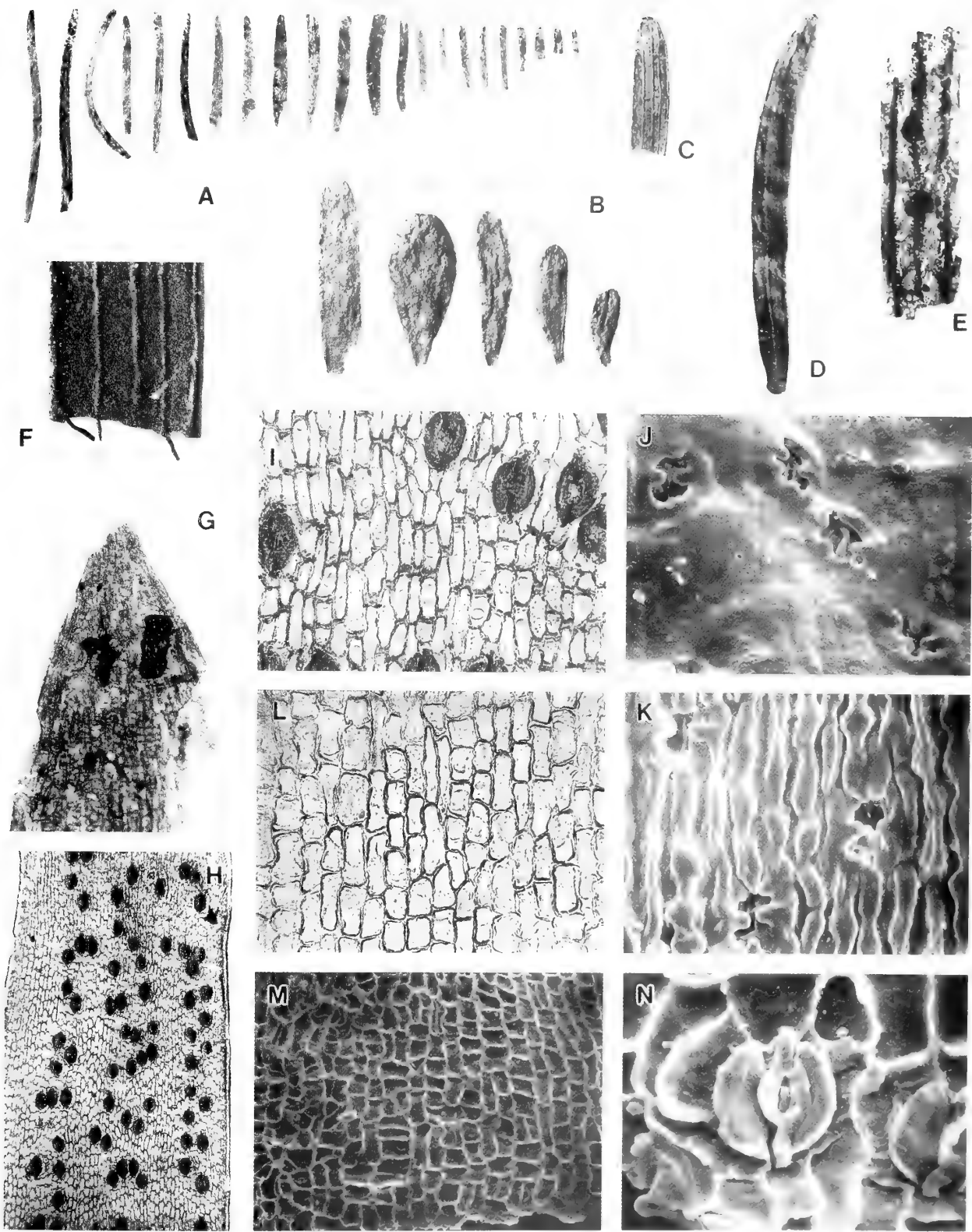
1852   *Pinites Linkii* (Römer) Ettingshausen: 27. [Name change only]

1871   *Abietites Linkii* pro parte (Römer), emend. Schenk: 241, pl. 39; pl. 40, figs 1–5, 7. [Northwest Germany]

1923   *Podozamites* sp. cf. *affinis* (Schenk) Lipps: 356, text-fig. 25. [Northwest Germany]

1926   *Pityophyllum crassum* Seward: 106, text-fig. 16. [Western Greenland]

1936   *Abietites Linkii* (Römer); Michael: 61, pl. 3, figs 1, 2. [Northwest Germany]

1960   *Torellia*-aehnliche Daber: 606, pl. 15, figs 3a, 5. [Wilsnack borehole, Northeast Germany]

1961   *Abietites linkii* (Römer); Benda: 624, pls 39–41. [Northwest Germany]

1969   *Pseudotorellia heterophylla* Watson: 248, pl. 6, figs 6, 7; text-figs 59–64. [England]

1969   *Tritaenia linkii* (Römer) Mägdefrau & Rudolf: 296, text-figs 1–5. [Northwest Germany]

1976   24 GINK ToB Oldham [Code used instead of Linnean binomial]: 458, pl. 68, figs 1–3. [England]

1976   25 GINK ToA Oldham [Code used instead of Linnean binomial]: 458, pl. 68, figs 4–8. [England]

1980   *Pseudotorellia*-aehnliche Daber: 276, pl. 106, fig. 3; text-fig. 109. [Gorlosen and Wilsnack boreholes, Northeast Germany]

1984   *Abietites linkii* (Römer); Van der Burgh & Van Konijnenburg-Van Cittert: 390, pl. 9, fig. 1. [Northwest Germany]

1991   *Tritaenia linkii* (Römer) sensu Mägdefrau & Rudolf; Bose & Manum: 14.

1991   *Tritaenia crassa* (Seward) Bose & Manum: 15, fig. 6. [Western Greenland]

1991   *Tritaenia linkii* (Römer); Wilde: 366, figs 1–3.

1996   *Abietites linkii* (Römer); Watson & Alvin: 9. [Name in list].

1996   *Pseudotorellia heterophylla* Watson; Watson & Alvin: 9. [Name in list].

1998   *Pseudotorellia linkii* (Römer) Watson & Harrison: 241, figs 1A, B; 3; 4A–J; 5–10; 11A–G; 12–15; 16D; 20A, B.

2000   *Tritaenia linkii* (Römer); Manum, Van Konijnenburg-Van Cittert & Wilde: 262, fig. 2; pl. 1, figs 1, 2, 6; pl. 2, figs 1, 3, 4.
        Tritaenia crassa (Seward); Manum, Van Konijnenburg-Van Cittert & Wilde: 263, pl. 1, fig. 5; pl. 2, fig. 2.

DIAGNOSIS.   See diagnosis of *Pseudotorellia linkii* (Römer) given by Watson & Harrison (1998: 242) which requires no emendation at present.

NEOTYPE AND TYPE LOCALITY.   Specimen 1997/102, Museum für Naturkunde, Berlin. Collected Gothan 1940, Osterwald, northwest Germany; selected and figured by Watson & Harrison (1998, figs 5C, 7E, F).

MATERIAL AND OCCURRENCE.   *Pseudotorellia linkii* (Römer) (1839) in the needle-leaved form occurs in great abundance at some localities in the Wealden of northwest Germany (Wilde 1991; Watson & Harrison 1998; Manum *et al.* 2000) with elliptical leaves in Germany occurring as a rare hand specimen and in boreholes. In the English Wealden *P. linkii* occurs mainly from debris deposits but also as single needles on some of the hand specimens collected by Rufford. In the Weald Basin it has been isolated from plant debris beds in the Ashdown Beds Formation at Ecclesbourne Glen and Fairlight where needles and elliptical leaves have been found in the same samples (Watson 1964, 1969), and Oldham (1979) recorded the species from Haddock's Rough and Galley Hill. In the Wessex Basin much more
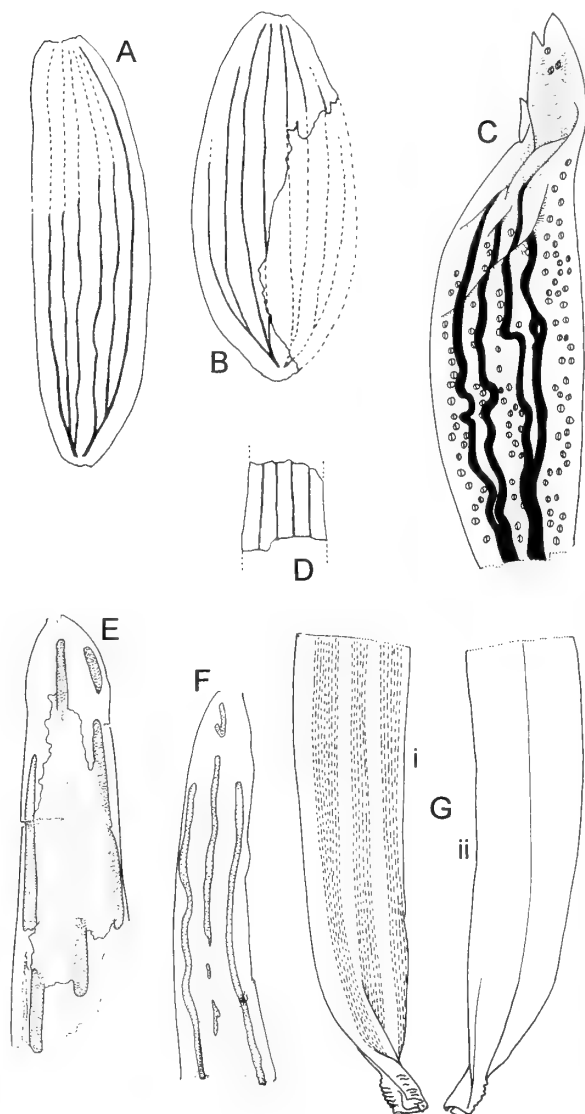
Fig. 23 A–G   *Pseudotorellia linkii* (Römer) Watson & Harrison. **A, B,** wide elliptical leaves from the English Wealden. A, V.51525; **B,** V.51528; **C,** leaf showing two dichotomising veins and positions of stomata, V.64243, × 15; **D,** part of sub-parallel-sided leaf with 4 veins, V.51527; **A, B, D** after Watson 1969, all × 10; **E,** distal part of leaf with 3 resin canals, V.64239, × 10; **F,** distal leaf fragment with 3 resin canals, V.64240, × 10; **G,** leaf with twisted, wrinkled base; **i,** lower surface showing position of 3 stomatal bands; **ii,** upper surface with grooved midline, V.64250, × 6.

extensive material has recently been recovered from several plant debris horizons in the 'lignite beds' of Arkell (1947) at Worbarrow Bay, Dorset. *P. linkii* has also been recognised in the Lower Cretaceous flora of Angiarsuit, western Greenland (Seward, 1926). The specimens shown in Figs 22 and 23, from England, Germany and Greenland, are all housed in the NHM (see Appendix).

DESCRIPTION.   The extensive study of *Pseudotorellia linkii* (Römer) by Watson & Harrison (1998) involved bulk maceration of many samples from both England and Germany with the isolation of large numbers of individual leaves displaying a considerable range and

variety of leaf size and shape. The leaf outlines fall into two groups, those which are needle-like (Figs 22A, C, D; 23D, E, F, G) and those which are more or less elliptical (Figs 22B; 23A–C). The former are largely the leaves originally described as the conifer *Abietites linkii* (Römer) and the latter more or less represent the material which was described by Watson (1969) as a new species of *Pseudotorellia*, but which also included needle-like leaves known to have two or more veins. Wide, elliptical leaves are well-known from the German Wealden but Watson & Harrison's (1998) identification and interpretation of the German specimens has been rejected by Manum *et al.* (2000), largely on the basis of the needle leaves and the elliptical leaves occurring separately and at different stratigraphic horizons. However, since Manum *et al.* (2000) have refrained from presenting cuticle evidence (a cornerstone of Mesozoic palaeobotany) in support of this rejection, we are unable to accept their alternative thesis at present. The salient features of the recombined species *P. linkii* (Römer), based on English and German material, are summarised below.

The needle leaves are parallel-sided (or sub-parallel) with a tapering or rounded apex (Fig. 22A, C, D) and sometimes a twisted base (Figs 22A 4th from right; 23D, E). The known width of needles is 1 to 3 mm but relatively few whole needle leaves have been recovered (Fig. 22A far left, D). The known length to width ratio in needles is 8:1 in the shortest (Fig. 22A sixth from right) and just over 20:1 in the longest (Fig. 22A extreme left). The veins in long needles have been repeatedly demonstrated as at least two in number but some needle leaves as narrow as 1.4 mm certainly have up to four (Fig. 22E).

The elliptical leaves show a wide variety of shape and size (Figs 22B; 23A–C) with a known range of 4 to 8 mm wide and 10 to 40 mm long, plus one exceptionally large leaf from Germany which is 15 mm wide and 60 mm long (Watson & Harrison 1998, figs 4A, B; 6M). The shape of the broader leaves of *P. linkii* varies from sub-parallel (Fig. 22B left) through well-formed ellipses (Fig.23A, B) with symmetrical distal and proximal halves, to obovate with a broad, blunt apex (Fig. 22B second from left).

Watson & Harrison (1998) have discussed and speculated about the significance of the heterophylly and the probability that the two leaf forms represent juvenile and adult foliage of one tree species. They suggested that the wide leaves are more likely to be juvenile and the needle leaves adult. However, the evidence remains slim despite the huge array of *P. linkii* leaves available. Watson & Harrison's (1998: 247) reasons hinge upon the wider leaves (which are far fewer in number in the leaf deposits) having great variation in shape and size, which could indicate the unsettled morphology of juvenile foliage and might also reflect a probable wide ancestral form. Some modern conifers such as *Juniperus* have large juvenile and small adult foliage. The needles of *P. linkii*, which occur in vastly larger numbers than wide leaves, are more consistent in shape and size, suggesting the stable morphology of leaves in the main part of the plant. Smaller leaves are of course a more advanced character in conifers.

The extreme tip of the leaf, which was possibly scarious, is almost always missing (Fig. 23A, B, F, G) but a rare example of a leaf with an intact, pointed tip is shown in Fig. 22G. The bases of both the needles and the wider leaves sometimes show twisting and/or transverse wrinkling, thought to be related to post-mortem shrinkage of a triangular leaf-base with the apex and two sides disposed adaxially, and the base of the triangle abaxially. Some well-preserved *P. linkii* leaves reveal this triangular cross-section, with the apex in the centre of the upper surface and a flat lower surface (see Watson & Harrison 1998, fig. 9F, G) and despite not having been found connected to a shoot, there seems to us little doubt that the triangular leaf-bases were attached to the shoots of *Sulcatocladus robustus* Watson &

Harrison (1998) in life. The two are repeatedly associated and their remarkably similar cuticles possess the same unusual, distinctive characters.

The cuticle of *P. linkii* is extremely thick (15–50 µm) on both leaf surfaces with stomata restricted to the abaxial surface, unrelated in arrangement to the position and number of veins which vary from 2 to at least 12, according to the width of leaf. The leaf base shows the entry of two veins which give rise to branches on their inner sides (Fig. 23A–C) in the lower part of the leaf. Distally beyond the branching the veins run parallel to one another (Figs 22C, F; 23A–D) then converge towards the apex. The veins are more resistant to maceration than the mesophyll and can easily be seen as black strands if maceration is halted before completion (Figs 22E; 23A–C). Brittle, amber-coloured strands of resin, which fluoresce under ultraviolet light, appear to be infills of resin canals running unbranched along the full length of the leaf, each strand lying directly beneath a stomatal band (Fig. 23F, G).

Fig. 22L, M shows the upper cuticle devoid of stomata, with square to rectangular epidermal cells arranged in longitudinal files, and the characteristic pairs of cells which underwent late division (Fig. 22M). The upper cuticle is typically smooth on the outer surface but commonly has hemispherical cuticular thickenings or pustules (Fig. 22L) on the inside surface of the outer periclinal walls, particularly near the leaf base.

Ordinary epidermal cells of the lower cuticle are similar in size to those of the upper epidermis and are also arranged in longitudinal files (Fig. 22H, I), though less strictly amongst the stomatal bands. The outside surface of the lower epidermis is very variable, sometimes as smooth as in Fig. 22J, sometimes with weakly developed cuticular ridges running along the length of a file of cells (see Watson & Harrison 1998, fig. 13B) or with very strongly developed ridges as in Fig. 22K. Fig. 22I shows the same distinctive pustules on the inside of the ordinary epidermal cells as occur in the upper cuticle. Stomata are absent from the extreme base of the leaf but 2 or 3 distinct stomatal bands (Fig. 23G) are initiated just above the base (see Watson & Harrison 1998, fig. 8C), generally remaining distinct until about half way up the leaf (Figs 22H), then merging distally into a single broad band (Watson & Harrison 1998, fig. 8A) which continues to the apex. Occasionally the stomata are arranged in one broad longitudinal band, more often in the wide elliptical and obovate leaves (Watson & Harrison 1998, fig. 11G) than in needle leaves. The stomata are all longitudinally aligned and have a more or less rectangular pit, usually overhung by subsidiary cell papillae (Figs 22J, K), but are occasionally smooth-rimmed. Aborted stomata, with single, undivided guard cell mother cells are a common feature in leaves of *P. linkii* from all localities. Figs 22H, I, N show the distinctive, thickly cutinized, dorsal plates of the guard-cells, with their typical long, strongly cutinized polar appendages.

DISCUSSION. The revision of this species by Watson & Harrison (1998) united three separate species from Lower Cretaceous floras of England, Greenland and Germany. The evidence for this comes largely from the cuticle, which is identical in all three floras, but also from the discovery that the long-known German Wealden needles attributed to *Abietites linkii* Römer (1839) did not possess a single-veined 'midrib' as had long been supposed. The recognition in all the leaves of parallel, dichotomising veins ending freely in the distal margins, led to the newly combined species being assigned to the genus *Pseudotorellia* Florin and removed from the Ginkgoales with tentative reattribution to the Coniferales, supported by the associated *Sulcatocladus* shoots.

The leaves of *P. linkii* were almost certainly deciduous and Watson & Harrison (1998) have discussed the evidence for this. The presence
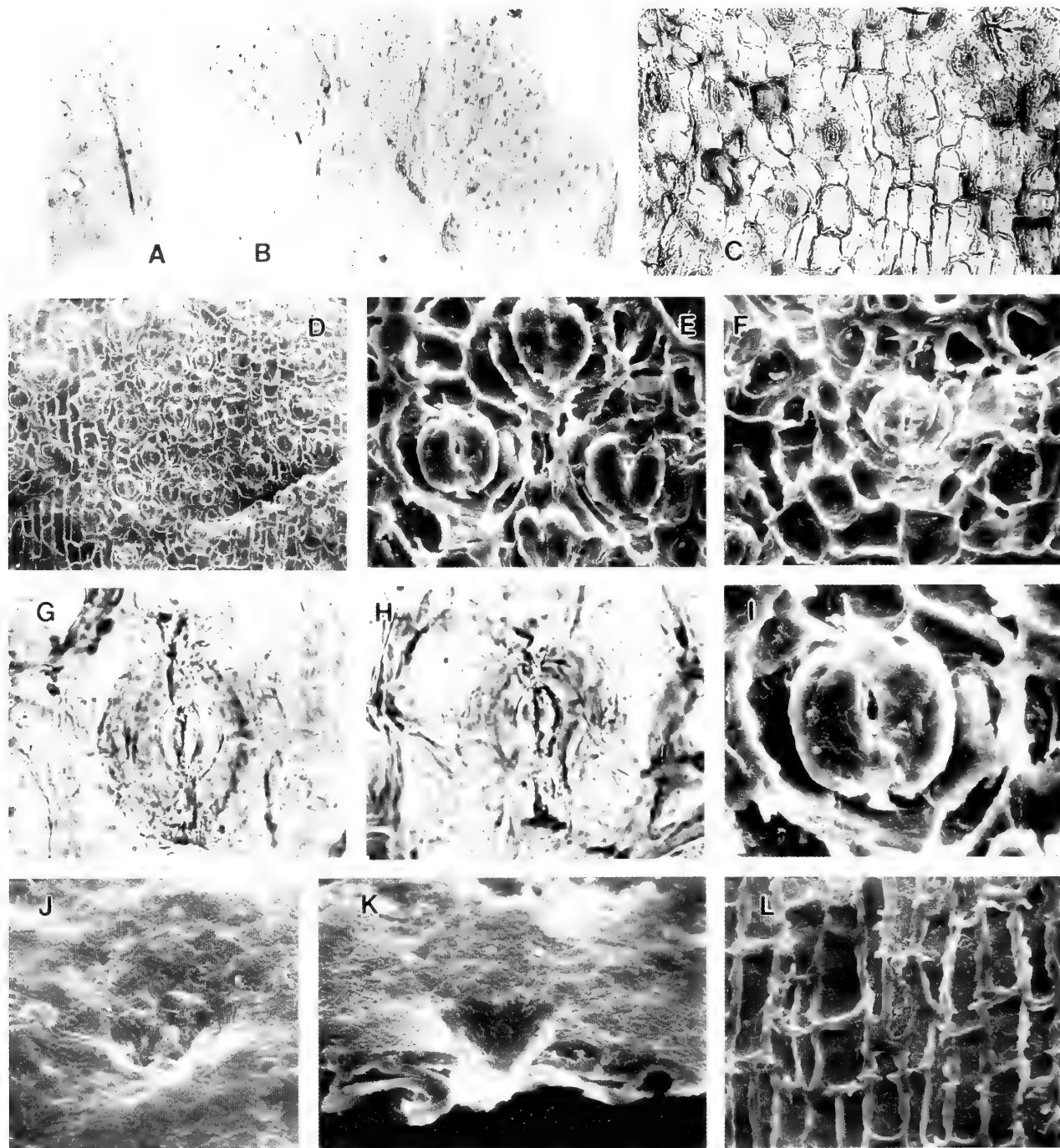
Fig. 24 A–I   *Pseudotorellia vimesiana* sp. nov. **A**, apical portion of leaf with tip missing, LM, V.64554, × 25; **B, holotype**; leaf fragment opened up to show stomata confined to one surface (?lower), V.64555, × 25; **C–L**, all from V.64556; **C**, lower cuticle with stomata, LM, × 125; **D**, inside surface of lower cuticle showing stomata arranged in three indistinct bands, SEM, × 75; **E**, four stomata viewed from the inside, SEM, × 250; **F**, single stoma viewed from the inside surrounded by rings of subsidiary and encircling cells, SEM, × 250; **G, H**, stomata showing oval rim to pit (in top plane of focus) and polar appendages to guard cells (in lower plane of focus), LM, × 500; **I**, stoma viewed from the inside with distinct cutinization of ventral as well as dorsal periclinal walls of guard cells, SEM, × 500; **J**, crater-like stomatal pit, SEM, × 500; **K**, cut section through a stomatal pit, SEM, × 500; **L**, inside surface of upper cuticle showing outlines of rectangular cells and longitudinal bars, SEM, × 250.

of a scar at the base of the leaf and the occurrence of *P. linkii* needle leaves in concentrated deposits (brachyblasts of Vakhrameev 1971) in the Wealden of northwest Germany are thought to indicate seasonal leaf abscission. *Sulcatocladus robustus* shoots (Watson & Harrison 1998), first attributed to this species by Dunker (1846: 18), and later by Wilde (1991) but not separately named, are regarded as

the shoots from which the leaves were shed and Fig. 32 shows reconstructions of them bearing the two leaf forms of *Pseudotorellia linkii*.

Pseudotorellia vimesiana sp. nov.   Figs 24, 25

1969   Unnamed conifer, Mägdefrau & Rudolf: 297, text-fig.6. [Wealden, North West Germany].

DIAGNOSIS.   Leaf parallel sided for much of its length; up to at least 17 mm long, 0.5–1.7 mm wide; tapering to acute apex; base shortly attenuate. 2 resin canals present in some leaves. [Veins not discerned.]

Cuticles about 10 μm thick; upper usually slightly thicker than lower. Upper cuticle without stomata. Upper epidermal cells arranged in longitudinal files, rectangular or square; late division pairs of cells common. Cells 35–170 μm long (mean length 87 μm); divided cells generally 8–27 μm wide (mode 17 μm); ordinary cells 30–65 μm wide (mode 38 μm). Anticlinal walls generally 3–12 μm wide, becoming wider near leaf-base; straight or slightly undulating; frequently pitted. Surface walls flat and of uniform thickness; finely pitted on outside or longitudinally striated, striations not restricted to one cell. Papillae and trichomes absent. Hypodermis usually present. Hypodermal cells arranged in longitudinal files; square or rectangular and elongated transversely, occasionally triangular; 40–115 μm long (mean length 65 μm) × 50–115 μm wide (mean width 78 μm).

Lower cuticle with stomata arranged in 2 or 3 bands near leaf-base, merging to a single broad band distally. Stomatal density inside bands 50–110 per mm² (mean density 73 per mm²). Ordinary epidermal cells arranged in longitudinal files; files may or may not be slightly disrupted in stomatal bands. Cells between stomatal bands rectangular, 45–190 μm long (mean length 123 μm) × 15–30 μm wide (mean width 22 μm). Cells within stomatal bands 3, 4 or 5-sided, elongated longitudinally or isodiametric or, very occasionally, wider than long; 20–130 μm long (mean length 63 μm) × 20–60 μm wide (mean width 29 μm). Longitudinal bars rare. Anticlinal walls 3–8 μm wide, becoming wider near leaf base; straight or slightly undulating; occasionally pitted. Outer periclinal walls usually flat and of uniform thickness, rarely with faint median longitudinal ridge on outside; outer surface finely pitted or, on some leaves, striated. Striations longitudinally aligned, not restricted to one cell. Papillae and trichomes absent. Hypodermis frequently present beneath ordinary epidermal cells, absent beneath stomatal apparatus. Hypodermal cells arranged in longitudinal files, generally square or rectangular and elongated transversely, usually 45–65 μm long × 35–70 μm wide.

Stomata longitudinally orientated. Stomatal apparatus 68–152 μm long (mean length 104 μm) × 45–95 μm wide (mean width 73 μm). Stomatal pit with smooth oval rim. Inner anticlinal walls of subsidiary cells broad, inwardly sloping to form crater-like pit with small hole at base. Subsidiary cells arranged in a ring around the pit; 2 polar and 2, 4 or rarely 6 lateral; none bearing papillae. Encircling cells occasionally present laterally. Guard cell pair slightly sunken beneath subsidiary cells; 38–80 μm long (mean length 57 μm) × 27–65 μm wide (mean width 38 μm); dorsal plates thickly cutinized, axe-head shaped; T-pieces thinly cutinized; ventral walls not preserved or sometimes thinly cutinized.

NAME.   After Sir Samuel Vimes, commander of the Ankh-Morpork City Watch in the Discworld novels of Terry Pratchett.

HOLOTYPE & TYPE LOCALITY.   V.64555, Fig. 24B, a leaf from debris beds in the Wessex Formation at Mupe Bay, Dorset. Wessex Formation, Barremian.

MATERIAL & OCCURRENCE.   The species is known in dispersed material from the Ashdown Beds Formation at Hastings, the Wessex Formation at Mupe Bay in Dorset and the Wealden leaf coal of Düingen, North West Germany. It has also been recognised amongst the NHM Seward collection from the Lower Cretaceous of Western Greenland.

DESCRIPTION.   The leaves of *Pseudotorellia vimesiana* sp. nov. are some of the smallest assigned to the genus *Pseudotorellia*. They appear to have been needle-like in form with slightly constricted bases and, according to Mägdefrau & Rudolf (1969: 297), have sharply pointed apices. Two unbranched resin canals have been recognised in some leaf fragments from Western Greenland (Fig. 25A, B), one running close to each lateral margin and avoiding the stomata arranged in a single band. Other more complete leaves described below reveal that the stomata are arranged in two or three bands near the leaf base, merging into one in the more distal regions. Some of the leaves exhibit a faint differentiation of the upper epidermal cells along the midline. These cells are narrower and more elongate than usual. The rectangular outline of all the upper epidermal cells and their arrangement in longitudinal files is shown in Figs 24L and 25D. The latter also illustrates the high proportion of cells which are split into pairs by late cell division. Each member of the pair is about half the width of most other cells and the paired cells generally having a width between 8 and 27 μm, the most common value being 17 μm; the unpaired cells being 30–65 μm wide with a width of 38 μm recorded most frequently.

The anticlinal walls of the epidermal cells are frequently traversed by straight pits seen in Fig. 25D which also shows the finely cutinized outlines of the larger, transversely elongate, hypodermal cells. Such cutinization is only irregularly developed and inner periclinal cutinization of the epidermal cells is very rare. Fig. 24J shows the generally flat outer periclinal walls of the epidermal cells, which are of uniform thickness.

Fig. 24B, D shows that, as in all species of *Pseudotorellia*, the stomata of *P. vimesiana* are restricted to the lower leaf surface where they are always orientated longitudinally. Fig. 24D also shows the stomata arranged in three bands at the leaf base. They do however, gradually merge into a single broad band in the distal part of the leaf. The margins of the bands are characteristically indistinct in Fig. 24D; although the ordinary lower epidermal cells have a tendency to be shorter and wider within the stomatal bands than between them, the change is not an abrupt one. The ordinary cells near the leaf base on both surfaces are considerably smaller, more square and have far thicker anticlinal walls than those elsewhere (as in *Pseudotorellia linkii*). Fig. 24J, K shows the finely pitted outside surface of the cuticle, but in some cuticles (e.g. Fig. 25C) this pitting is replaced by longitudinal striae. The hypodermal cutinization which is frequently present beneath the epidermal layer is shown in Fig. 24F. The stomata of *P. vimesiana* are small and quite closely packed together (Fig. 24B–E). The thickly cutinized dorsal plates make the stomata conspicuous in the light microscope (Figs 24C, G, H; 25E, F) and from the inside in the SEM (Fig. 24E, F, I), but from the outside in the SEM they are quite inconspicuous (Fig. 24J, K), the stomatal pits being crater-like (Fig. 24K) and lacking a distinct rim. The inwardly sloping walls converge towards the little hole at the bottom of the pit, which is shown most clearly in Fig. 25F. This figure also shows that the wide inner anticlinal walls of the lateral subsidiary cells may easily be confused in the light microscope with the dorsal plates of the guard cells which underlie them. The dorsal plates are generally wider than the inner anticlinal walls of the subsidiary cells so that only the guard cell thickenings can be seen on the inside of the cuticle with the SEM (Fig. 24I). The party wall between the guard cell pair
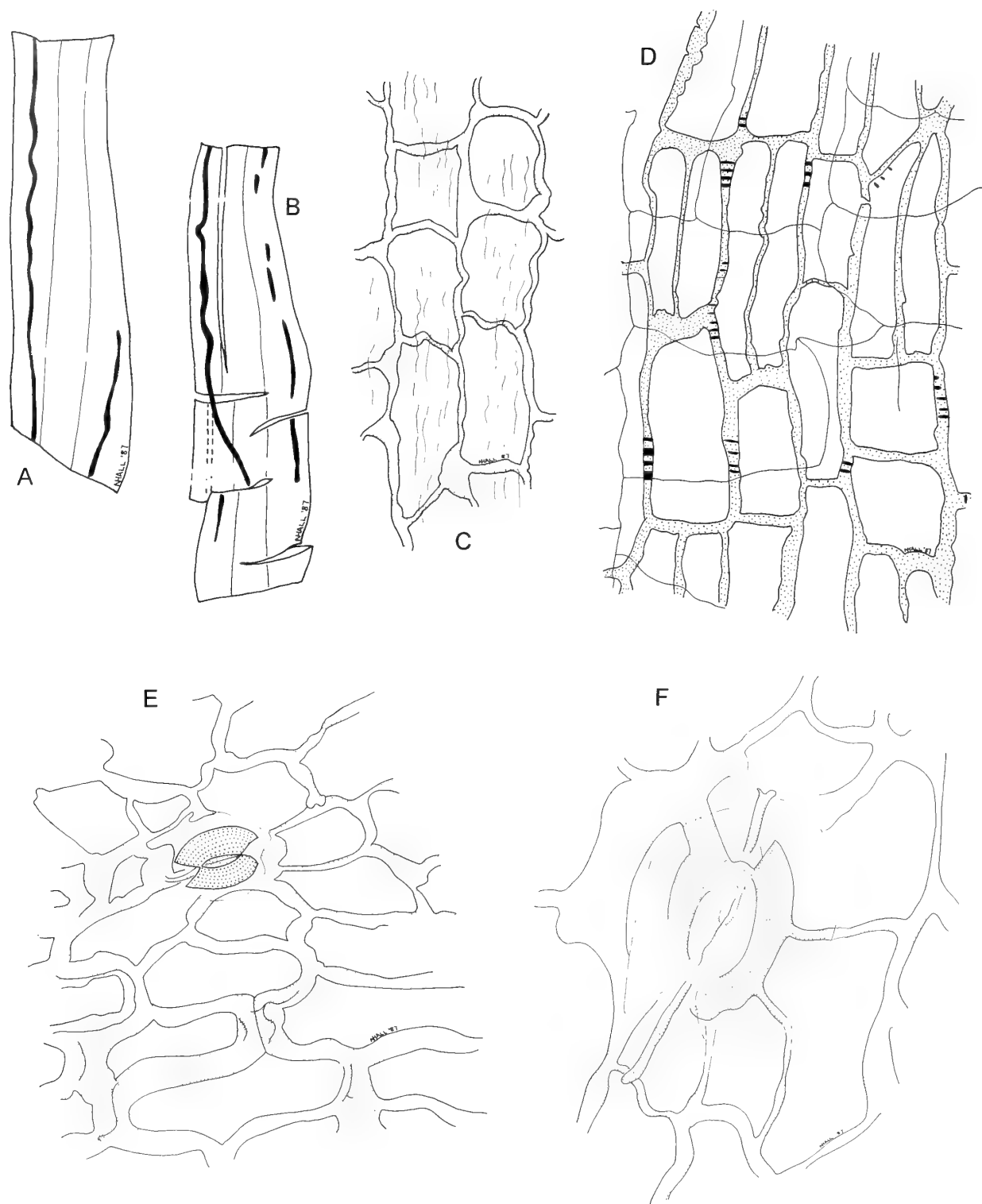
Fig. 25 A–F   *Pseudotorellia vimesiana* sp. nov. **A, B,** leaf fragments showing resin canals and stomatal bands. **A, B,** V.20434 from the Lower Cretaceous of Western Greenland. × 15; **C,** lower cuticle. Ordinary epidermal cells with longitudinal striations over outside surface, English Wealden, V.64557, × 400; **D,** upper cuticle showing epidermal cells arranged in longitudinal files frequently split into pairs, pits in anticlinal walls, finely cutinized outlines of hypodermal cells, Wealden of Hastings, V.64558, × 400; **E, holotype,** lower cuticle showing a single stoma with conspicuous guard cell dorsal plates, V.64556, × 400; **F, holotype,** single stoma with wide inner anticlinal walls to subsidiary cells, guard cell dorsal plates and polar appendages conspicuous, V.64556, × 800.

is thinly cutinized beyond the dorsal plates, resulting in fully devel-
oped T-pieces or polar appendages (Figs 24G, I; 25E, F). The ventral
wall of the guard cells is also frequently represented in the fossil as
a thin sheet of cuticle (Fig. 24I).

DISCUSSION AND COMPARISON. *Pseudotorellia vimesiana* sp. nov.
was first recorded as an unnamed leaf sample in the Wealden leaf
coal of Düingen, North West Germany (Mägdefrau & Rudolf 1969:
297), where it occurs alongside the larger and much more numerous
leaves of *Pseudotorellia linkii* (Römer) Watson & Harrison (1998).
It is formally diagnosed and named here for the first time.

   P. vimesiana is readily distinguished, by the small size of its
leaves, from the two other species of *Pseudotorellia* which are
known to occur in the German Wealden leaf coal, *P. linkii* and a new
undescribed species (Watson *et al.* in preparation). The leaves of *P.
vimesiana* never exceed 1.7 mm in width and the stomata have guard
cells generally less than 60 μm long beneath oval, crater-like pits.
Nevertheless, several features suggest a close affinity with
Pseudotorellia linkii: the arrangement of stomata in two or three
bands in the leaf base merging distally into one band; the thick
cutinization of the anticlinal walls around the leaf base; the presence
of resin canals. It is mainly this similarity with *P. linkii* which leads
us to assign this species to *Pseudotorellia*, since no evidence of veins
has been found. It should be noted however that isolated distal leaf
fragments with a single median stomatal band and resin canals
present certain difficulties of generic assignment and, for example,
those in Fig. 25A, B could have been readily attributed to
Sciadopityoides without evidence from other specimens. The prob-
lems associated with generic usage for this group of leaves is
discussed below in the account of *Sciadopityoides*.

Form-genus *SCIADOPITYOIDES* Sveshnikova

1981   *Sciadopityoides* Sveshnikova: 1722.
1987   *Sciadopityoides* Sveshnikova; Manum: 159.
1990   *Sciadopityoides* Sveshnikova; Bose & Manum: 21.

TYPE SPECIES. *Sciadopithys uralensis* Dorofeev & Sveshnikova
1959: 1277; pl.2, figs.1–7.

DIAGNOSIS. [based on Sveshnikova 1981 (in Russian) with slight
emendments] Leaves linear, lanceolate or more broadly elliptical.
Apex obtuse or acuminate. Cells of the upper epidermis, and of the
lower in lateral areas outside median stomatal zone, seriately arranged,
without papillae. Lower surface of leaf with a median stomatal zone,
which may or may not be in a groove. Epidermal cells of stomatal
zone less seriately arranged than in rest of leaf. Stomata monocyclic,
longitudinally or transversely orientated or with no preferred orien-
tation. Subsidiary cells 4 to 6, but may be up to 9. Subsidiary and
non-stomatal cells inside groove with or without papillae.

DISCUSSION. Sveshnikova (1981) erected the form-genus
Sciadopityoides to accommodate all Mesozoic conifer-like leaves
which resemble the living *Sciadopitys* inasmuch as they have a
median stomatal band, but with no natural affinities implied and in
practice evidence of familial position is usually completely lacking.
Thus *Sciadopityoides sensu* Sveshnikova became a useful form-
genus for leaves of this type with stomata confined to a band along
the middle of the lower surface (Hall 1987; Manum 1987) and of
probable conifer affinity, though sometimes with characters reminis-
cent of the Ginkgoales (see comments by Watson & Harrison 1998).
This is the sense in which *Sciadopityoides* is used here. However,
several other genera have subsequently been erected (Reymanówna
1985; Bose & Manum 1990, 1991) which overlapped with

Sciadopityoides and changed its usage. In particular Bose & Manum
(1990) undertook an extensive study and reassessment of
'*Sciadopitys*-like' leaves from the Mesozoic of northern Europe and
established a new conifer family, the Miroviaceae, containing sev-
eral new leaf genera, including *Mirovia* Reymanówna (1985) but
without evidence from reproductive structures. It is interesting to
note that Reymanówna (1985) considered *Mirovia* to be close to
Pseudotorellia and probably ginkgoalean.

   In the genera assigned to the Miroviaceae Bose & Manum (1990,
1991) and Manum *et al.* (2000) have given considerable weight to
the presence of a median groove or line of differentiation on the
upper epidermis which they take as circumstantial evidence for a
double vein such as occurs in the leaves of *Sciadopitys verticillata*,
a unique feature amongst living conifers. However, *Pseudotorellia
linkii* (Römer) often has such a midline feature on leaves (Fig. 22D;
see also Watson & Harrison 1998) with numerous dichotomising
veins. Furthermore, the leaves of *Abies* and similar modern conifers
often display such a midline groove over their single vein (Watson &
Harrison 1998, figs 1D, 2A–D). It thus seems unwise to regard the
presence of such a feature in fossil leaves as in any way indicative of
leaf venation.

   It has become clear that there are numerous Mesozoic species of
the *Sciadopityoides* and *Pseudotorellia* type, variously referred to
the Coniferales or Ginkgoales, with a distinctive suite of characters
in common. Many of them are known to be heterophyllous with both
needle-like and more or less elliptical leaves; some are associated
with and/or attributed to shoots of the *Sulcatocladus* type. The
shared features of these plants might well indicate a family relation-
ship, almost certainly coniferous, but conclusive evidence from
reproductive structures is entirely lacking. Therefore in the absence
of any positive evidence of this kind we propose to include Wealden
leaves with a median stomatal band in the form-genus *Sciadopityoides
sensu* Sveshnikova (1981).

Sciadopityoides greeboana sp. nov.   Figs 26–30

1976   27 GINK GkA Oldham (Code used in place of Linnean
       binomial): 460; pl.70, figs 3–6; pl. 71, figs 1, 3, 5.

DIAGNOSIS.   Leaf linear, up to at least 9 mm long, 0.5–1.5 mm
wide. Apex acute, frequently missing. Base slightly constricted. 2–3
resin canals present in some leaves, longitudinally aligned,
unbranched.

   Upper cuticle 5–20 μm thick, stomata usually absent, very
occasionally one or two stomata present on whole leaf. Epidermal
cells arranged in longitudinal files; rectangular or square; generally
35–115 μm long × 15–40 μm wide; along midline narrower and more
elongate; near leaf base, shorter, as little as 5 μm long. Longitudinal
bars between pairs of cells common. Anticlinal walls generally 5–10
μm thick, straight or slightly sinuous; near leaf base, 10–20 μm wide,
strongly sinuous. Outer periclinal walls 5–17 μm thick, of uniform
thickness or, more commonly, with a solid, median, longitudinal
ridge over a file of cells, occasionally restricted to one cell, rarely
longitudinal rows of hollow papillae take the place of ridges; outside
surface finely pitted; inside surface finely granular. Inner periclinal
walls 0.5–1.0 μm thick. Hypodermis usually present. Hypodermal
cells approximately square, 23–46 μm long × 27–46 μm wide;
arranged in longitudinal files; anticlinal walls frequently sinuous.

   Lower cuticle with stomata confined to a median band, sometimes
in a groove. In lateral, stomatal-free zones, cuticle 5–20 μm thick;
epidermal cells similar shape, size and arrangement to those of upper
surface; hypodermis present. Stomatal band 1/3–2/3 of total leaf
width; tapering to a point just below leaf apex; cuticle 3–8 μm thick.
Ordinary epidermal cells in stomatal band, arranged in longitudinal

files, not disturbed by stomata; usually four-sided, elongate, end
walls transverse or oblique, generally 20–150 μm long × 8–19 μm
wide; anticlinal walls straight, 1–4 μm wide; median longitudinal
ridge over outside of one or several cells in a file, alternatively, ridge
broken up into a row of small solid circular thickenings. Hypodermis
absent. Stomata longitudinally aligned and elongated, arranged in
longitudinal files; density 80–125 per mm^2 (average 92 per mm^2).
Stomatal pit spindle-shaped, rim smooth; flanked on each side by
one, or rarely two, subsidiary cells with domed or thickened surface
walls; one subsidiary cell at each pole, indistinct from ordinary
epidermal cells. Encircling cells frequently present. Guard cells
slightly sunken; pair of dorsal plates 34–57 μm long × 27–50 μm
wide, thickly cutinized, thinning slightly towards aperture, inner
anticlinal walls shallowly cutinized; polar appendages present but
variable in development; ventral plates very occasionally cutinized
adjacent to aperture.

NAME.   After Greebo, Nanny Ogg's cat in the Discworld novels of
Terry Pratchett.

HOLOTYPE & TYPE LOCALITY.   V.64560, Fig. 26A (middle top
row), F. A dispersed leaf fragment from Galley Hill, East Sussex.
Ashdown Beds Formation, Berriasian.

MATERIAL AND OCCURRENCE.   *Sciadopityoides greeboana* sp. nov.
is known only from dispersed material in the English Wealden. It was
first recognised by Oldham (1976) from the Wessex Formation of
Worbarrow Bay, Dorset, and in the Ashdown Beds Formation at
Ecclesbourne Glen near Hastings and Galley Hill, East Sussex. It
was also found in Cuckfield No.1 Borehole, Sussex. The species has
also been collected by Watson and co-workers from other debris
partings along the Hastings coastal section. Stratigraphical range:
Berriasian-Hauterivian.

DESCRIPTION.   The leaves of *Sciadopityoides greeboana* sp. nov.
are needle-like with a distinct median stomatal band on the lower
surface (Figs 26F; 27A–O), sometimes in a groove. The wide sto-
matal band accounts for one to two thirds of the total leaf-width. The
cuticle of the stomatal band is relatively thin and tends to be easily
damaged, so that in many specimens only the upper cuticle and the
stomatal-free edges of the lower cuticle are preserved intact. The leaf
is parallel-sided for much of its length, but tapers to an acute, slightly
asymmetrical, apex with the stomatal band pinching out to a point
just below the apex of the leaf (Fig. 27B, E, F, J, K). The extreme tip
of the leaf, however, is frequently missing (Figs 26C; 27B, E, J, K).
The leaf is slightly contracted at its base (Figs 26E, 27H) but the
width of the stomatal band remains the same; thus taking up almost
the entire width of the leaf in its basal part. The leaves often contain
two or three maceration-resistant strands, one down each side of the
stomatal band and usually a third along the midline (Figs 26 B; 27C–
G, M). These resinous strands, which are amber in colour and
fluoresce in ultraviolet light, are interpreted as the infillings of resin
canals.

Both cuticles of this species are very brittle. The upper (adaxial)
cuticle is the thicker of the two and stomata are usually absent,
although an occasional stray one has been observed (Fig. 29A). The
ordinary epidermal cells, which form well defined longitudinal files,
are rectangular or square with thin, slightly sinuous outlines. At the
leaf base, however, the cells are much shorter and have very wide
anticlinal walls which are strongly sinuous. Along the full length of
the leaf, the cells over the midline are clearly differentiated; being
distinctly narrower and more elongate than normal (Fig. 29A).
Throughout the upper epidermis, late-division cell pairs split by
longitudinal walls are common. The epidermal cells may have flat,
uniformly thickened surface walls but solid longitudinal ridges are
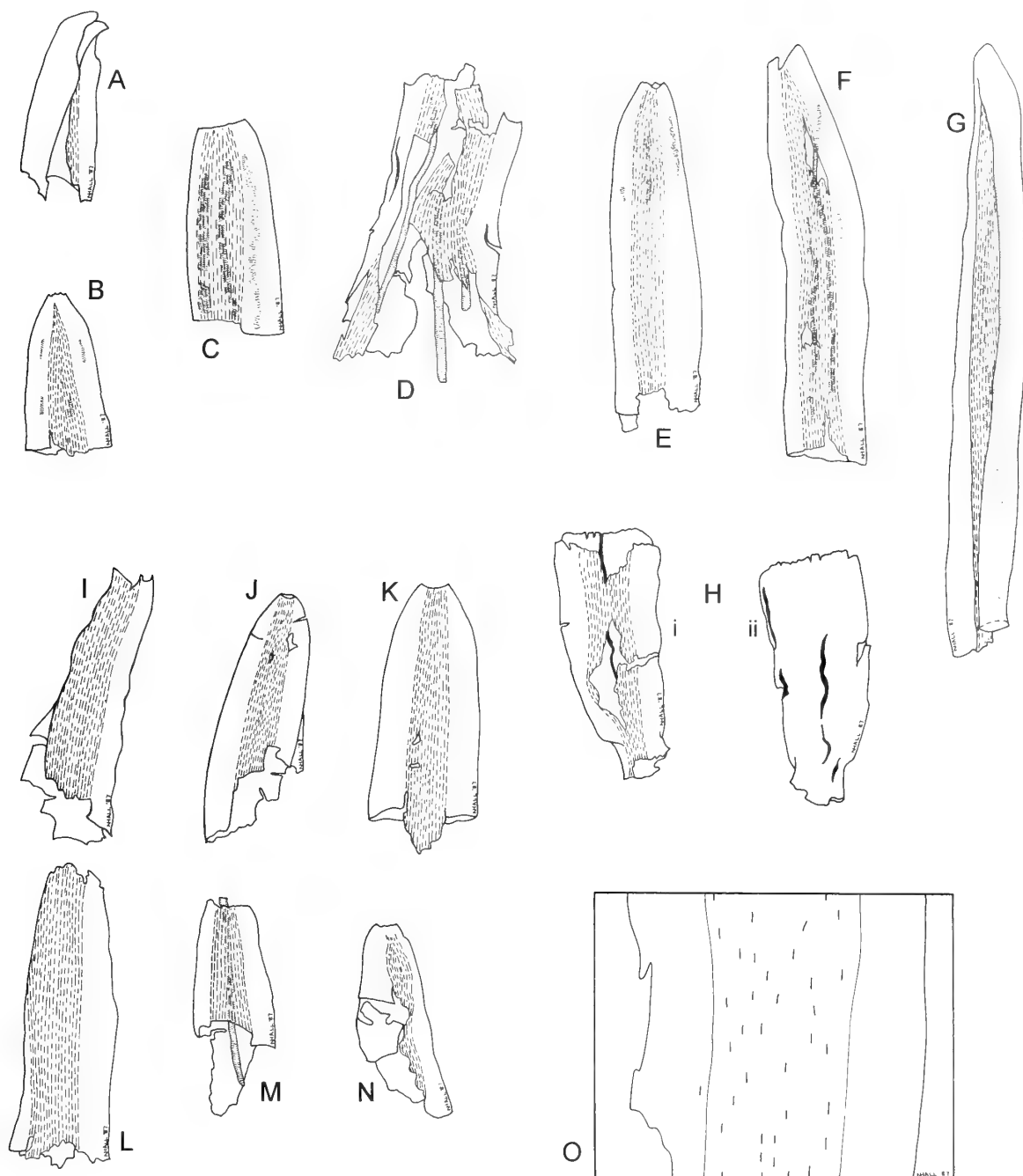
Fig. 27 A–O *Sciadopityoides greeboana* sp. nov. All dispersed portions of leaves from the Fairlight Clay at Galley Hill, East Sussex. **A–G, I–N,** apical fragments with lower side uppermost to show position of stomatal band (dashed) and resin canals (dotted); **Hi, ii,** lower and upper surfaces of proximal portion of leaf with constricted base; **A–N,** V.64572–64585, all × 15; **O,** distribution of stomata in a band on the lower cuticle, V.64586, × 50.

also common, extending the length of one or more cells in a file (Figs 28B; 29B), less commonly, hollow dome-like papillae are present (Fig. 29C). Beneath the thickly cutinized outer periclinal walls of the epidermal cells, a thin layer of cuticle representing the inner periclinal wall is frequently developed (Fig. 29D). The outlines of the hypodermal cells are also usually preserved as thin sinuous strands of cuticle (Figs 28B; 29E, F). The hypodermal cells are commonly twice the width of the epidermal cells and often have their longitudinal walls directly beneath those of the epidermal cells. They are, however, shorter than the overlying epidermal cells and the end walls of the two cell layers are rarely in line.

On the lower leaf surface, the lateral, stomatal-free zones are identical to the upper cuticle. The stomatal band with its thinner cuticle is quite distinct and has clearly defined edges. Hypodermal cutinization is completely lacking. The ordinary epidermal cells in the band are also rectangular and arranged in files (Fig. 29A–D).
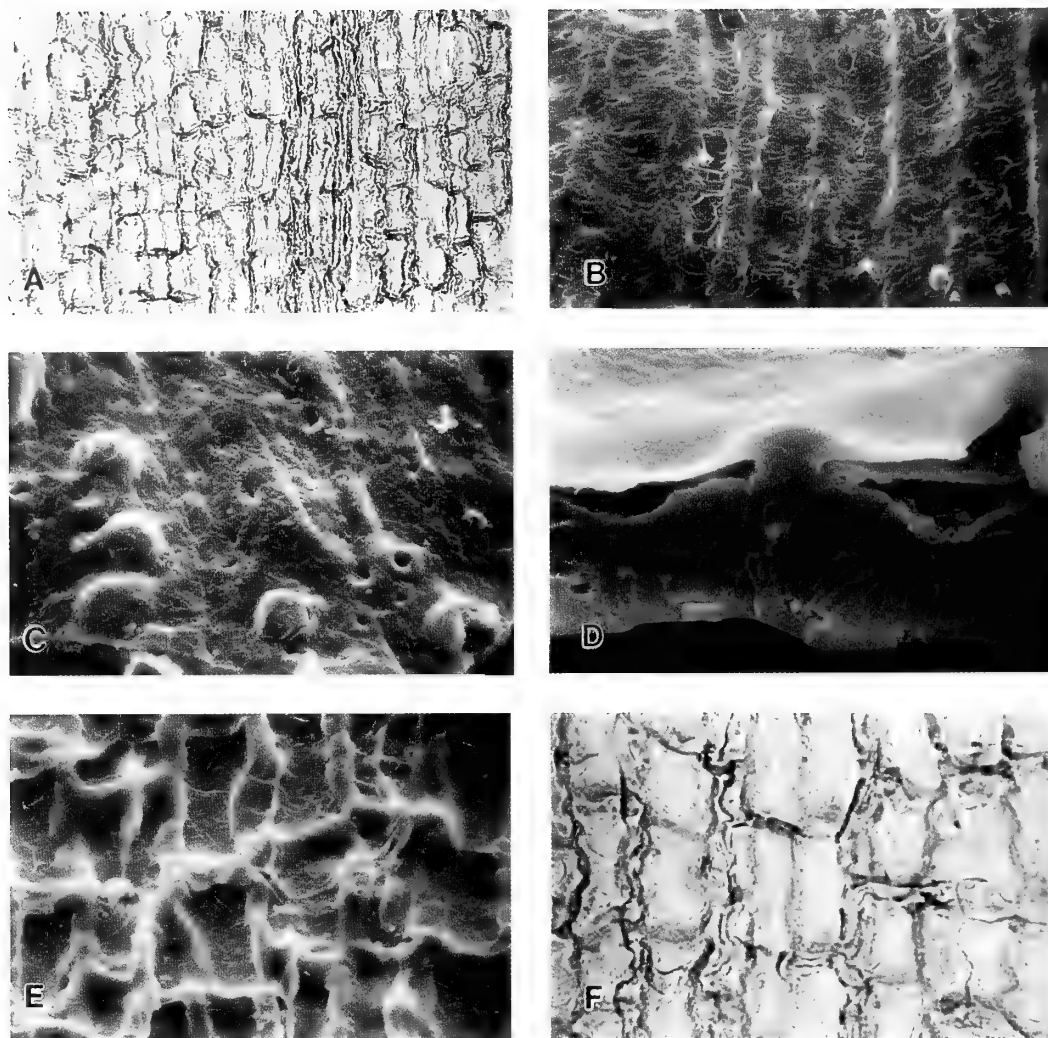
Fig. 28 A–F   *Sciadopityoides greeboana* sp. nov. All upper cuticles of dispersed leaves from the Fairlight Clay at Galley Hill, Sussex. **A,** cuticle showing narrow cells over the midline and one stray stoma, LM, V.64587, × 125; **B,** typical appearance of the outside surface with longitudinal ridges over files of epidermal cells, SEM, V.64588, × 125; **C,** less common appearance of the outside surface, with hollow papillae, SEM, V.64588, × 500; **D,** vertical section through upper cuticle (inside uppermost) showing thick outer and thin inner periclinal walls to epidermal cells, SEM, V.64588, × 2500; **E,** inside view showing hypodermal cutinization draped beneath epidermal cell outlines, SEM, V.64588, × 500; **F,** outlines of epidermal cells and larger hypodermal cells, LM, V.64587, × 300.

They differ from those of the stomatal-free regions in having domed outer surfaces and longitudinal ridges which are broad and often restricted to one cell (Fig. 29A–C, G). The ridges are frequently broken up into a row of small circular thickenings like a string of beads (Fig. 29A, C). The stomata themselves are also longitudinally aligned, although not forming distinct files (Figs 27O; 29A, B). The stomatal pits are spindle-shaped (Fig. 29E, G) and flanked by one or two elongate subsidiary cells on each side (Fig. 29F, H). The lateral subsidiary cells have domed surface walls (Fig. 29G, H) but usually lack any extra surface thickening. The polar subsidiary cells, one at each end of the pit, have a longitudinal ridge over the outside and are quite indistinct from the ordinary epidermal cells (Fig. 29D, F). The guard cells are sunken beneath the level of the subsidiary cells (Fig. 29D, F, H). They have strongly cutinized dorsal plates and at both

Fig. 29 A–H   *Sciadopityoides greeboana* sp. nov. All lower cuticles of dispersed leaves from the Fairlight Clay at Galley Hill, East Sussex. **A, B, E, F,** V.64587; **C, D, G, H,** V.64588. **A,** stomatal band with single bead-like papillae on the files of ordinary epidermal cells, LM, × 125. **B,** stomata with spindle-shaped pits and longitudinal ridges of thickening over ordinary epidermal cells, LM, × 250; **C,** outside surface of stomatal band with ridges and rows of papillae over the ordinary epidermal cells, SEM, × 250; **D,** inside surface of stomatal band showing longitudinal files of ordinary epidermal cells and longitudinally aligned stomata, SEM, × 250; **E,** stoma with outside surface of cuticle in focus. Stomatal pit spindle-shaped, longitudinal ridges on ordinary epidermal cells, LM, × 750; **F,** same stoma as Fig. E, with inside surface of cuticle in focus showing guard cells with strongly cutinized dorsal plates and polar appendages; one distinct subsidiary cell on each side of the guard cells, LM, × 750; **G,** stoma viewed from the outside with longitudinal ridges and distinct bead-like papillae on surrounding cells, SEM, × 750; **H,** stoma with ventral as well as dorsal cutinization of the guard cells, SEM, × 750.
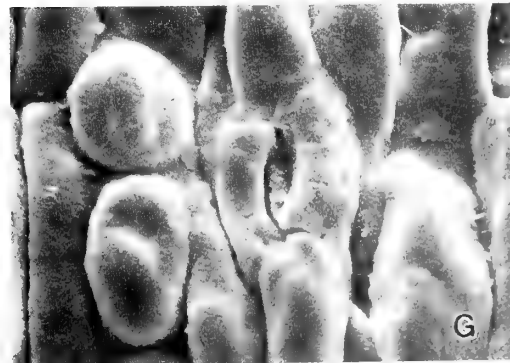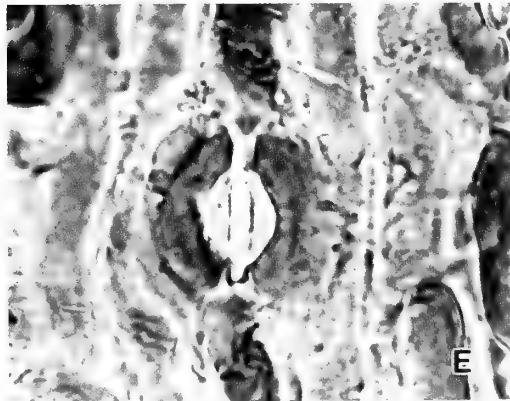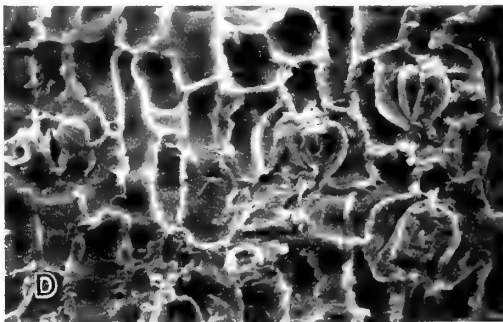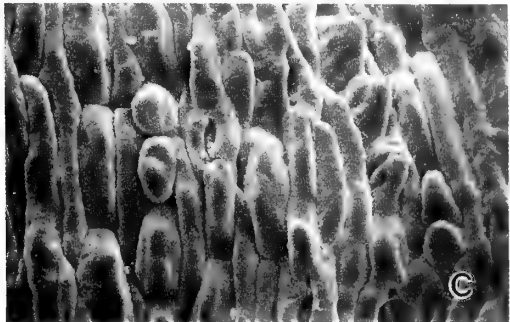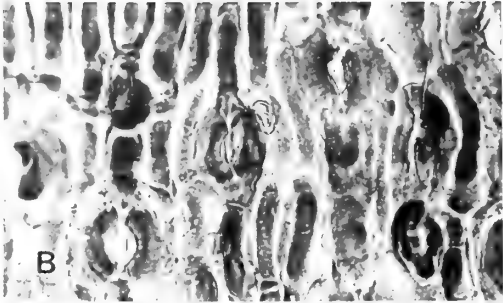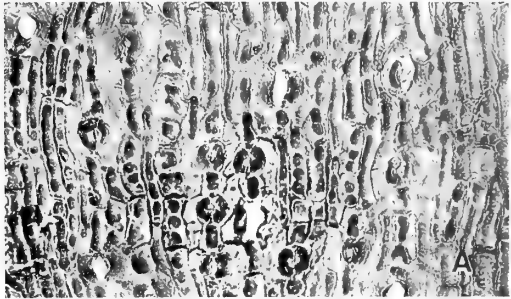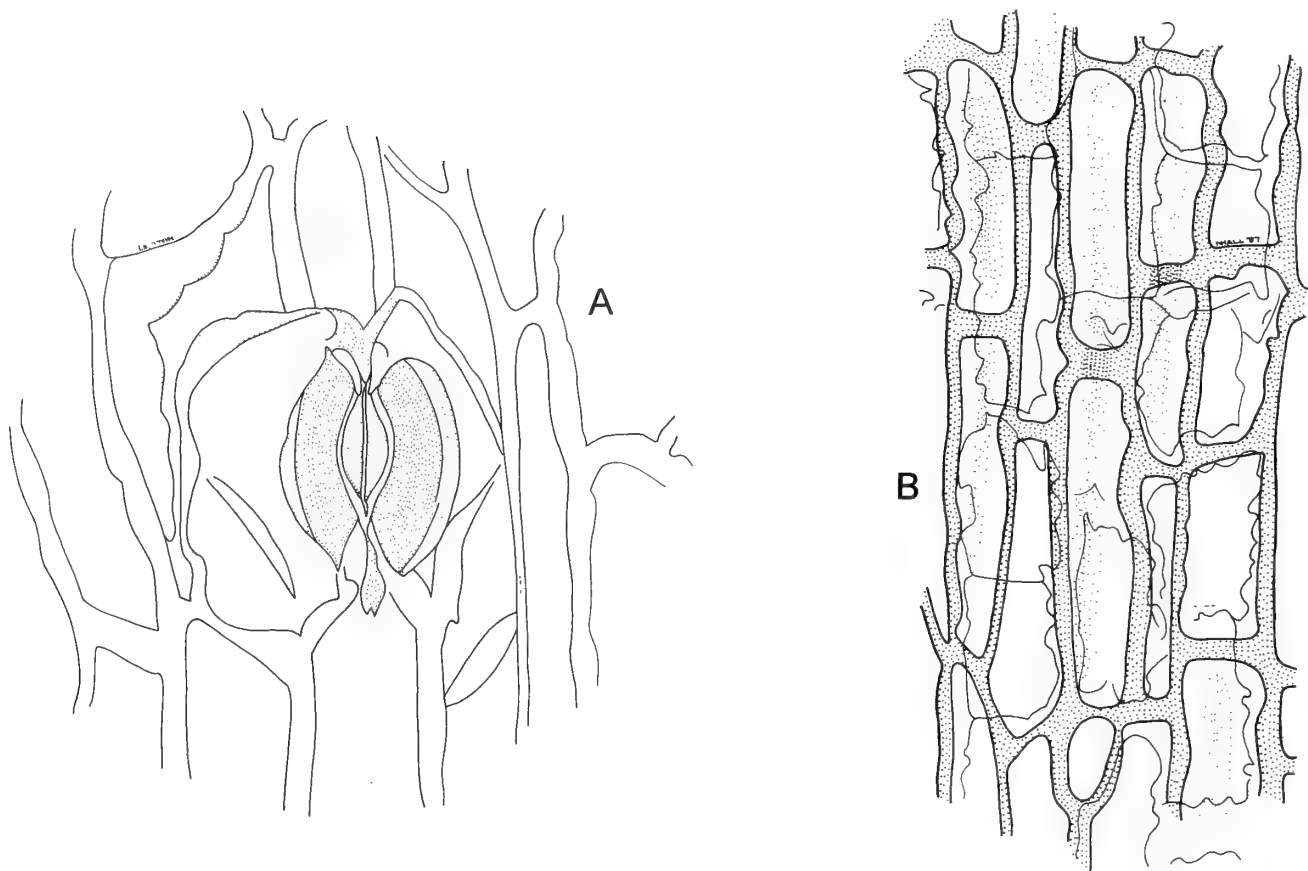
Fig. 30 A, B *Sciadopityoides greeboana* sp. nov. **A,** stoma viewed from the inside of the cuticle, V.64587, × 750. **B,** upper cuticle showing rectangular epidermal cells with median patches of thickening elongated longitudinally over one or more cells; thin sinuous outlines of hypodermal cells also shown, V.64587, × 400.

their inner and outer edges the guard cell anticlinal walls are shallowly cutinized (Figs 28A; 29F). Polar appendages are also a characteristic feature of this species but the extent to which they are developed is variable (Figs 28A; 29F). The ventral guard cell wall may also be partially cutinized in some stomata (Fig. 29D, H).

DISCUSSION AND COMPARISON.   When Oldham (1976: 460) first recorded the presence of this species in the English Wealden, he placed it tentatively in the Ginkgoales and remarked: 'this taxon is of ginkgoalean affinity but does not agree specifically with any of the published taxa'. However, the single median stomatal band occurring in these leaves suggests to us that it is appropriately assigned to the coniferous form-genus *Sciadopityoides* Sveshnikova. Of course no affinity with the living genus *Sciadopitys* is inferred and the family affinities of *Sciadopityoides greeboana* sp. nov. remain uncertain.

The leaves of *S. greeboana* are thought to have been spirally arranged on *Sulcatocladus* shoots which are described as a new species below. Attribution of the leaves of *S. greeboana* to shoots of *Sulcatocladus* is based on a constant association of the two species in the English Wealden and the strong similarities of their cuticles. Very similar shoots have been figured by Bose & Manum (1990, 1991) in association with *Sciadopityoides*-like leaves from the Lower Cretaceous of West Greenland, Spitsbergen and Arctic Canada.

The leaves of *S. greeboana* have many features in common with *P.*

linkii: a high frequency of leaves with broken apices; a differentiated midline on the upper epidermis; a tendency for epidermal cells to occur in pairs following late division; stomata which are always longitudinally aligned and restricted to the lower epidermis; guard cells with thickly cutinized, elongate dorsal plates, variably developed polar appendages and sometimes weakly cutinized ventral walls. It seems very likely that the two Wealden conifers belong to the same family. The case for including *P. linkii* in the Coniferales, possibly the Araucariaceae, has been discussed by Watson & Harrison (1998). The needles of *P. linkii* differ significantly in only two respects. Firstly, the stomata are arranged in three bands in the basal part of the leaf, although they merge into one broad band in the distal regions. Secondly, *P. linkii* is known to have several dichotomising veins although veins are not always preserved and their positions are not reflected in the epidermis. Numerous leaves of *P. linkii* had been examined and the species described several times before leaves with veins preserved in them were recognised (Watson & Harrison 1998). The possibility cannot therefore be ignored that *S. greeboana* might also have had more than one vein, thus reinforcing its affinities with *P. linkii*.

The reason why almost all the leaves have their tips missing remains a matter under discussion. Apart from *P. linkii*, similar proportions of leaves with missing tips have been recorded in *Sciadopityoides macrophylla* (Florin) Sveshnikova from the Jurassic of Norway (Manum 1987), *Bilsdalea dura* Harris (1979) from the
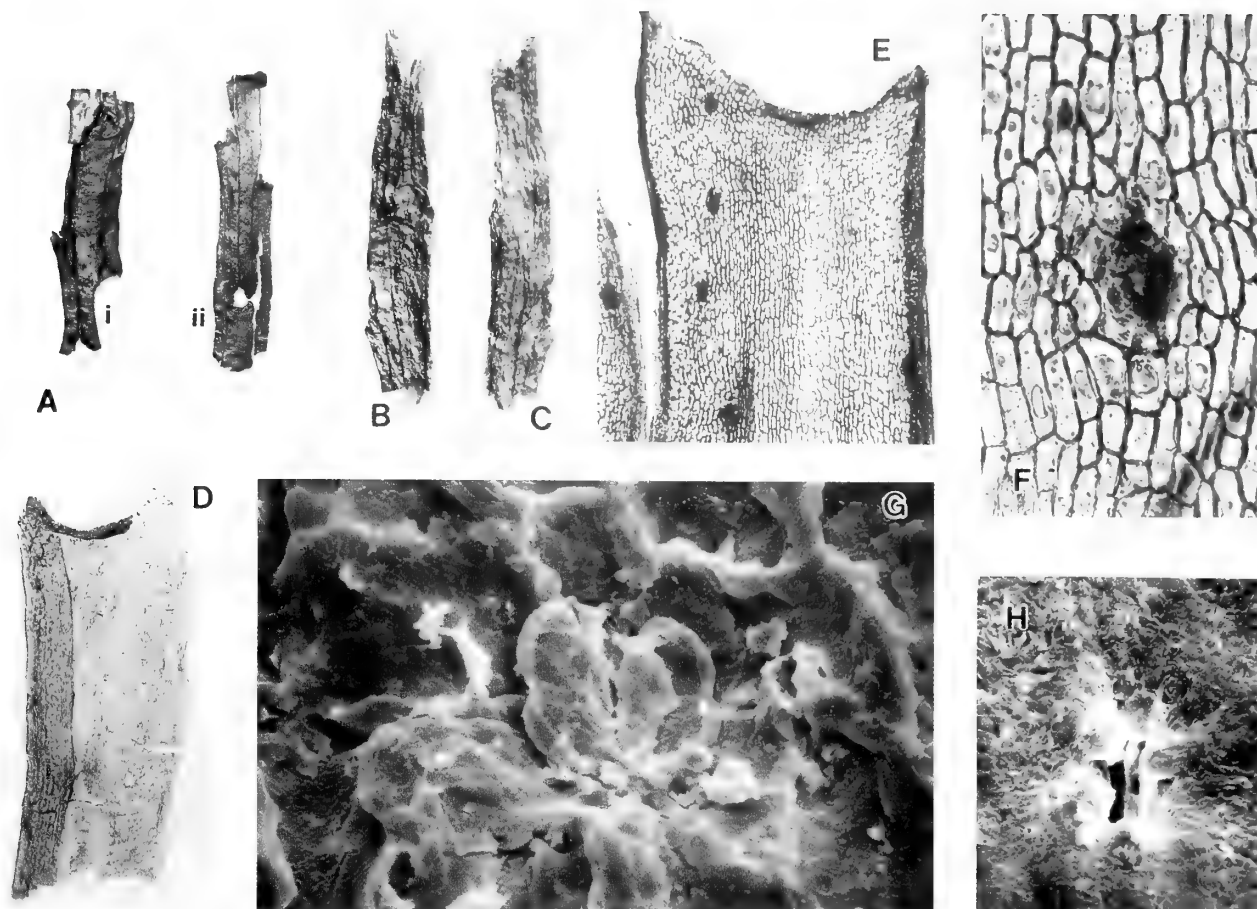
Fig. 31 A–H *Sulcatocladus robustus* Watson & Harrison. **A, B, C,** unmacerated shoot fragments showing leaf-scars and decurrent leaf-bases separated by sutures. **Ai,** V.64256; **Aii,** V.64257. Wealden, Düingen, North West Germany. × 2.5. **B, C,** two sides of same shoot from English Wealden at Worbarrow Bay, Dorset, V.64589, × 5; **D,** cuticle of decurrent leaf-base with lower margin of leaf scar at top, V.64590. Galley Hill, East Sussex. × 25; **E,** cuticle of decurrent leaf-base showing thinner cuticle of longitudinal sutures at each side. Indentation at top is lower part of leaf scar, V.64207, **holotype**. Wealden; Düingen, North West Germany, LM, × 60; **F,** stoma on leaf-base cuticle surrounded by epidermal cells with pustules, V.64207, **holotype**. Wealden; Düingen, North West Germany, LM, × 125; **G,** stoma viewed from inside showing cutinization of dorsal and ventral walls of guard cells, V.64291. Galley Hill, East Sussex, SEM, × 750; **H,** outside view of stomatal pit, overhung by subsidiary cell papillae, V.64292, dispersed cuticle from Wealden; Düingen. North West Germany, SEM, × 750.

Yorkshire Jurassic and *Mirovia szaferi* Reymanówna (1985) from the Jurassic of Poland. Manum (1987) suggested that nibbling by insects might be the explanation in *S. macrophylla*. Harris (1979: 138) entertained the possibility that the leaves of *B. dura* had a hydathode at the tip which would be easily lost during fossilisation. The expansion of the midrib in *B. dura* just below the tip appeared to support this but the vascular nature of the midrib has now been questioned (Watson & Harrison 1998) though this needs further investigation. Whatever the outcome for *B. dura*, there is no evidence to support the presence of terminal hydathodes in *S. greeboana* (or in *P. linkii*) and the lack of any insect damage elsewhere would appear to make Manum's suggestion unlikely. In the absence of any evidence to the contrary, it is suggested that the tips of the Wealden leaves were susceptible to damage as they were shed from the tree because they were very brittle, slender and probably scarious. The particularly brittle nature of the cuticle of *S. greeboana* rather supports this possibility. Reymanówna (1985: 7) noted that the intact, slightly pointed tips in unmacerated leaves of *Mirovia szaferi* lacked the lustre of the rest of the leaf and appeared to have much

thinner cuticle which disappeared upon maceration. A thick, black substance and swollen ends of resin ducts led her to suggest the possibility of resin being secreted through the leaf apex.

Genus *SULCATOCLADUS* Watson & Harrison

1998   *Sulcatocladus* Watson & Harrison: 263.

DIAGNOSIS.   [repeated from Watson & Harrison 1998] Shoots clothed with spirally-arranged, narrow, elongate, decurrent leaf-bases, each subtending a triangular foliage scar. Leaf-bases stomatiferous, separated by longitudinal, groove-like sutures.

TYPE SPECIES.   *Abietites linkii* (Römer) pro parte; emend. Schenk 1871: 241, pl. 39, fig. 6.

DISCUSSION.   *Sulcatocladus* is a genus recently erected by Watson & Harrison (1998) for coniferous shoots which consist largely of decurrent leaf-bases subtending leaf-scars, probably of deciduous leaves. Of the two distinct species identified so far, the one described

here as a new species can be attributed to the leaf species *Sciadopityoides greeboana* sp. nov. The other, *Sulcatocladus robustus* Watson & Harrison (1998), is attributed to the leaf of *Pseudotorellia linkii* (Römer) Watson & Harrison (1998). Both of the associated leaf species are described in the present work.

Sulcatocladus robustus Watson & Harrison   Figs 31–33

1846	Shoot associated with *Abietites (Abies) Linkii* (Römer) Dunker: 18, pl. 9, fig. 11e.
1871	*Abietites linkii* (pro parte Römer); emend. Schenk: 241, pl. 39, fig. 6.
1991	Twigs probably belonging to *Tritaenia linkii* (Römer); Wilde: 363, figs 4, 5.
1998	*Sulcatocladus robustus* Watson & Harrison: 264, figs 17A–I; 18A–D; 19A–H; 20A, B.

DIAGNOSIS.   See the original diagnosis of *Sulcatocladus robustus* Watson & Harrison (1998: 264) which requires no emendment at present.

HOLOTYPE AND TYPE LOCALITY.   V.64207, Fig. 31E, F from the Düingen leaf coal in the Wealden of northwest Germany.

MATERIAL AND OCCURRENCE.   *Sulcatocladus robustus* has been recognised from the Wealden of both England and Germany. Two German specimens and all the English material are housed in the NHM. Other specimens from Germany (e.g., Dunker Catalogue 70) are in the Museum für Naturkunde, Berlin.

DESCRIPTION AND DISCUSSION.   The shoots of *Sulcatocladus robustus* consist of helically arranged decurrent leaf-bases, each below a triangular leaf-scar. The phyllotaxis approximates to a 3/8 Fibonacci fraction resulting in the leaf-scars occurring at the junction of three decurrent leaf-bases (Figs 31Aii, 32A, B). This arrangement is reconstructed in Fig. 33. The decurrent bases are separated by groove-like sutures (Figs 31A–C, 32A–E) lined with fairly thin cuticle. Unbranched resin strands, often found inside the shoots (Fig. 32A, B), are interpreted as the infillings of resin canals and are the only recognisable remains of the internal shoot structure.

Sulcatocladus robustus has been attributed to the leaf species *Pseudotorellia linkii* (Römer) by Watson & Harrison (1998) on the basis of: the constant association of these two species in the Wealden of England and Germany; the perfect fit of leaf-base to leaf-scar; the similarity of their cuticles. Features shared by the two species include: thick cuticle, ordinary epidermal cells arranged in longitudinal rows; longitudinal striations on the inside surface of cell walls; cuticular pustules inside the cells on the outer periclinal walls; similar heavy thickening of transverse cell walls around the leaf-base and leaf-scar; stomata essentially similar with papillate subsidiary cells, guard cells with thickly cutinized dorsal plates, cutinized T-pieces associated with the polar appendages and sometimes partially cutinized ventral walls. As would be expected on a shoot, the stomata of *S. robustus* tend to differ from those of *P. linkii* in some features. The shoots have more subsidiary cells with thicker inner anticlinal walls, more deeply sunken guard cells and, sometimes, a ring of 10–12 encircling cells, thus making the stomatal apparatus rather larger than that on the foliage leaves. The triangular leaf-scar on *S. robustus* has been shown to match the bases of the *P. linkii* leaves (Watson & Harrison 1998), the known shoots being the right order of size to have borne the smaller, linear and lanceolate leaves. Assembled, green, leafy shoots have been reconstructed to show *S. robustus* bearing narrowly elliptical leaves (?juvenile) of *P. linkii* in Fig. 33A and needle leaves (?adult) in Fig. 33B.

It is clear that as the girth of the shoot increased the shoots would
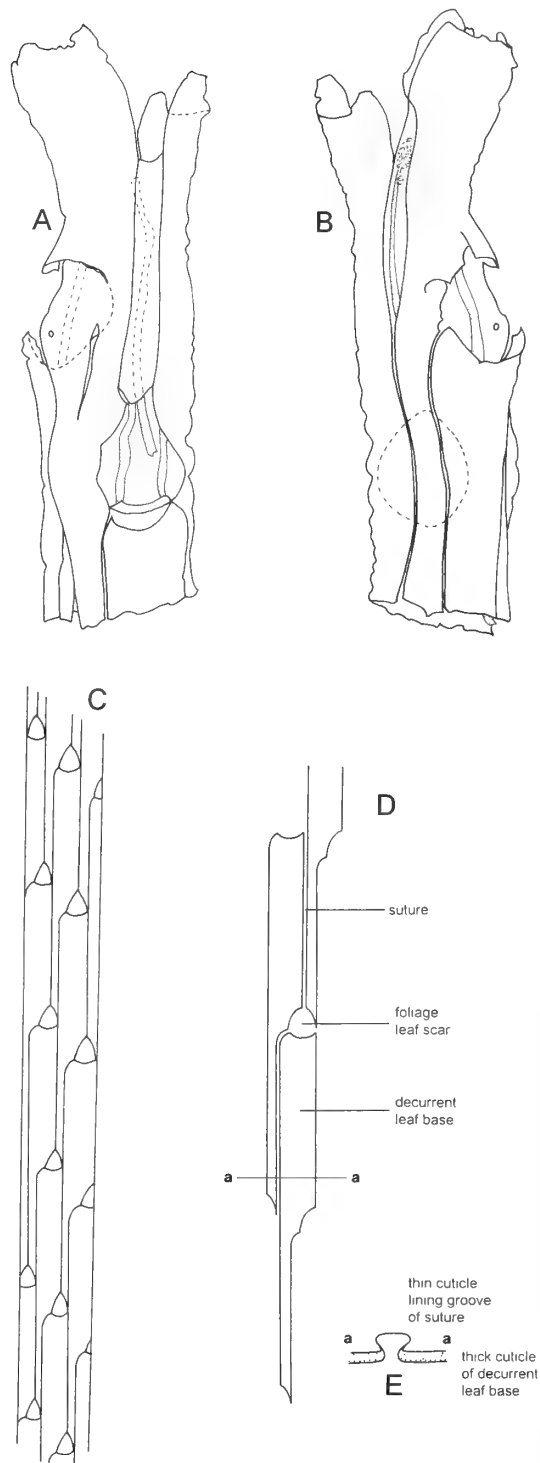
Fig. 32   *Sulcatocladus robustus* Watson & Harrison. **A, B,** two sides of same shoot fragment showing positions of leaf-scars and sutures. Three resin strands are present inside the shoot (stippled), V.64244, Haddock's Rough, Hastings, East Sussex, × 12; **C–E,** diagrammatic representation of *S. robustus* shoot. **C,** shows phyllotactic arrangement on one side of shoot, **D,** is labelled to show detailed relationship of a single leaf scar surrounded by 3 decurrent leaf-bases, **E,** is a transverse section along line a–a in Fig. D showing thin cuticle lining suture. C, D, × 4, E, not to scale.
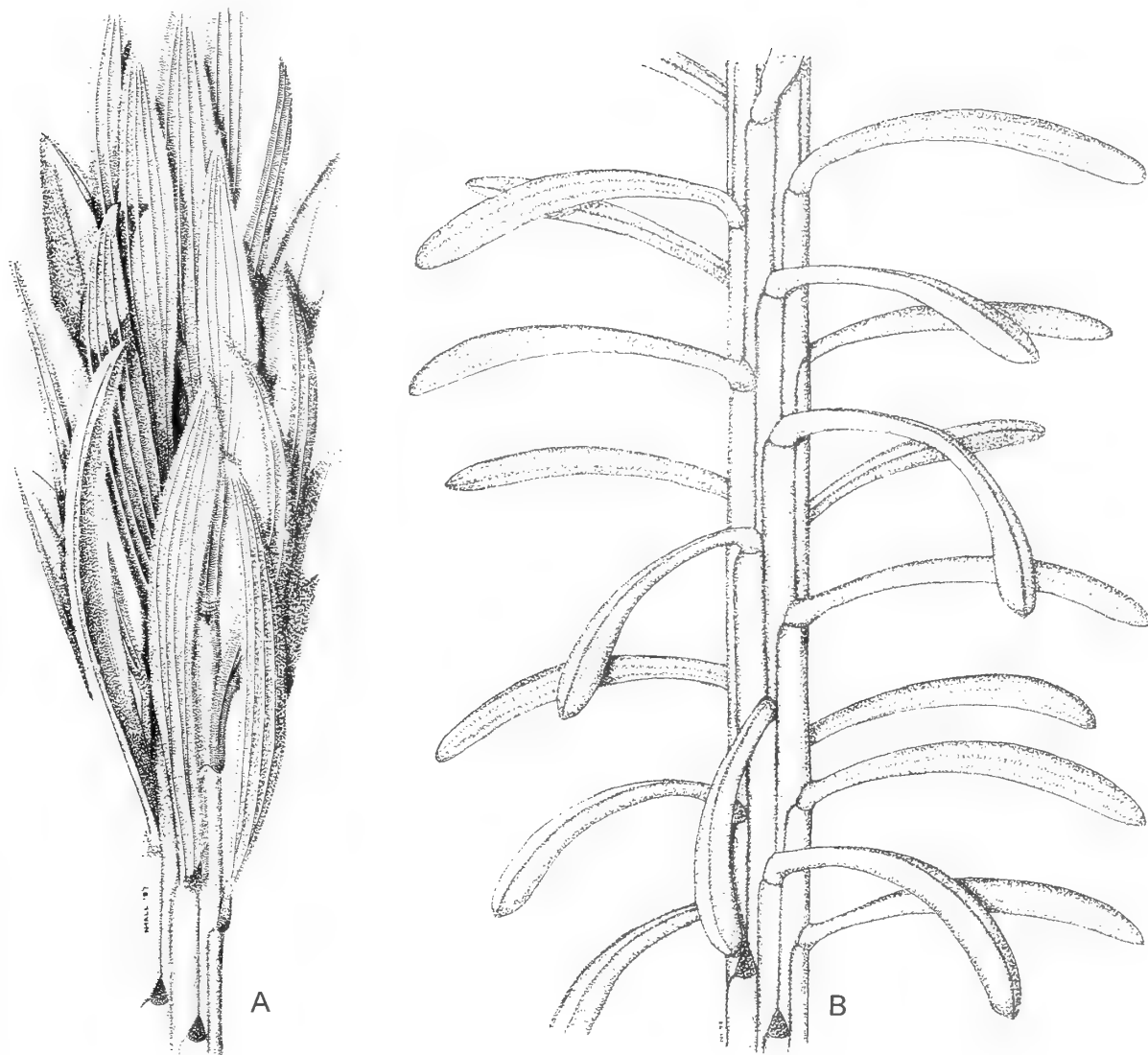
Fig. 33   Reconstructions of *Sulcatocladus robustus* bearing leaves of *Pseudotorellia linkii* (Römer) © Joan Watson & Nicola A. Harrison, 1998. **A**, shoot
bearing elliptical leaves, the possible juvenile foliage; **B**, shoot bearing needle leaves, the possible adult foliage; both approximtely × 2.5.

have become woody, as in living conifers. However, woody stems
have not been recognised in *S. robustus* which, like *P. linkii*, so far
occurs only as cuticular and resinous remains. We thus know nothing
of the older, thicker shoots of this species.

COMPARISON.   The two English species of *Sulcatocladus* are dis-
cussed below in relation to similar unnamed Mesozoic shoots and
their associated leaves.

Sulcatocladus dibbleri sp. nov.   Fig. 34

[Attributed to *Sciadopityoides greeboana* sp. nov. described above.]

DIAGNOSIS.   Shoots 1–2 mm wide. Decurrent leaf bases 0.3–1.0
mm wide × 4.0–5.0 mm long. Foliage leaf scars triangular, occurring
at junction of 3 decurrent leaf bases. Cuticle of decurrent leaf bases
about 10 μm thick. Ordinary epidermal cells arranged in longitudinal
rows; rectangular or square, generally 20–115 μm long (rarely up to
200 μm long) × 10–30 μm wide; square cells more common near

foliage leaf scar. Longitudinal ridges present over files of cells.
Papillae and trichomes absent. Hypodermis absent. Stomata longitu-
dinally orientated, restricted to zones adjacent to sutures, density up
to 15 per mm². Stomatal pit spindle-shaped, rim smooth; flanked on
each side by one or rarely two subsidiary cells with domed or
thickened surface walls; single undifferentiated subsidiary cell may
or may not be present at each pole. Encircling cells frequently
present. Guard cell pair slightly sunken; dorsal plates thickly cuti-
nized, isodiametric, 25–35 μm across; polar appendages usually
present; ventral walls frequently cutinized next to aperture.

NAME.   After C.M.O.T. Dibbler, sausage-in-a-bun purveyor of
Ankh-Morpork in the Discworld novels of Terry Pratchett.

HOLOTYPE AND TYPE LOCALITY.   V.64593, Fig. 34D–G, a shoot
collected by Oldham at Galley Hill, East Sussex. Ashdown Beds
Formation, Berriasian.

MATERIAL AND OCCURRENCE.   *Sulcatocladus dibbleri* sp. nov. has
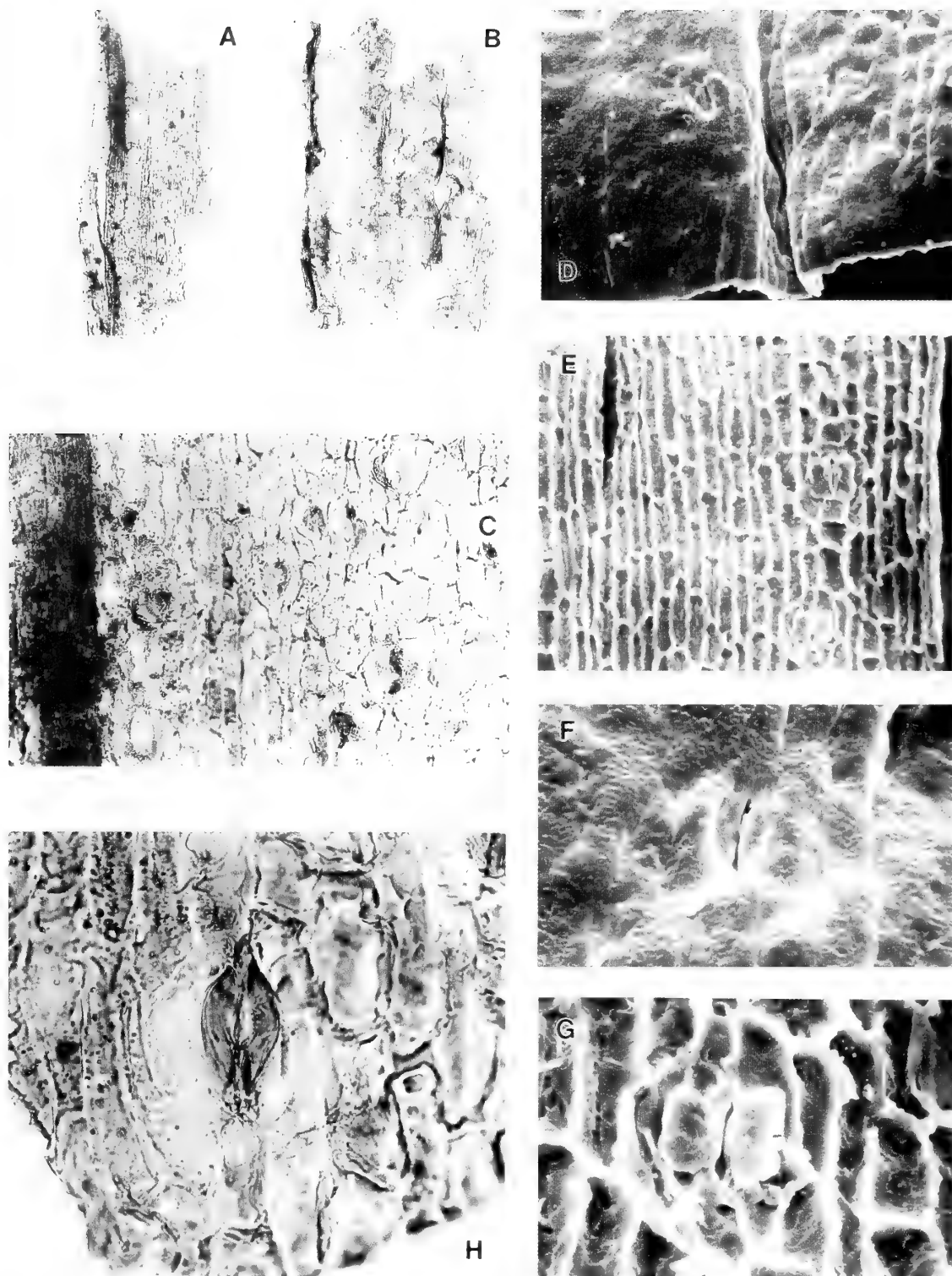
Fig. 34 A–H   *Sulcatocladus dibbleri* sp. nov. **A,** fragment of shoot showing two decurrent leaf bases separated by suture, V.64591, LM, × 25; **B,** shoot fragment with two sutures, V.64592, LM, × 25; **C,** cuticle of shoot in 34A showing longitudinally aligned stomata and fold with suture on left, V.64591, LM, × 125; **D–G,** holotype, V.64593; **D,** cuticle viewed from the outside showing separation of adjacent decurrent leaf-bases by a longitudinal, groove-like suture, SEM, × 250; **E,** decurrent leaf base cuticle viewed from the inside, showing stomata in a longitudinal row next to the suture, SEM, × 250; **F,** single stoma viewed from the outside, SEM, × 750; **G,** single stoma viewed from the inside, SEM, × 750; **H,** single stoma with prominent guard cells, large lateral subsidiary cells and small polar cells, V.64594, × 500.

been recognised amongst the dispersed cuticles collected by Watson (for Watson 1969) and Oldham (for Oldham 1976) from the English Wealden of Hastings and Galley Hill, East Sussex. Stratigraphic range: Berriasian.

DESCRIPTION.   Fig. 34D clearly shows the longitudinal suture between two decurrent leaf bases as a groove. Fig. 34A, C shows the suture on the left in a strong fold of cuticle. Fig. 34B has two sutures, one extreme left and another splitting open on right. Fig. 34E shows the rectangular outlines of the ordinary epidermal cells in longitudinal files and the fine pitting on the outside surface is visible in Fig. 34F. The stomata are typically longitudinally aligned and restricted to the areas adjacent to the sutures in Fig. 34D. Fig. 34F shows that the stomatal pit is spindle-shaped, flanked on either side by a ridge over the lateral subsidiary cells but with indistinct ends. Fig. 34H reveals the elongate lateral subsidiary cells and a single, poorly differentiated subsidiary cell at one pole. Only the dorsal walls of the guard cells are cutinized in Fig. 34G, although the ventral walls too are frequently cutinized in this species.

DISCUSSION.   *Sulcatocladus dibbleri* sp. nov. has been attributed to the needles of *Sciadopityoides greeboana* sp. nov. Although the needles have not been found attached, the two are constantly associated in the English Wealden and their cuticles are remarkably similar. *Sulcatocladus dibbleri* has rectangular epidermal cells arranged in files with faint longitudinal ridges over the outside surface, resembling those of the stomatal band in *Sciadopityoides greeboana*. The stomata, also longitudinally aligned, have spindle-shaped pits with smooth rims. One or two elongated subsidiary cells flank the sides of the pit and polar subsidiary cells, when present, are poorly differentiated. Guard cells too, are similarly cutinized. The fact that the leaves of *Sulcatocladus dibbleri* have never been found attached to the shoots of *Sciadopityoides greeboana* may be indicative of a deciduous habit, as suggested by Watson & Harrison (1998) and above for the very similar *Pseudotorellia linkii/Sulcatocladus robustus* complex. The reconstructed leafy shoot is envisaged as being similar to that of *Sulcatocladus robustus* sp. nov. and *Pseudotorellia linkii* (Römer) both for adult and juvenile foliage.

COMPARISON.   The cuticle of *S. dibbleri*, at about 10 µm thick, is much less robust than that of *S. robustus* which can be up to 50 µm but otherwise the shoots are very similar in construction. *S. dibbleri* and *S. robustus* are the only two species of the genus *Sulcatocladus* Watson & Harrison to have been named but it seems likely that some of the unnamed shoots associated with *Sciadopityoides*, *Pseudotorellia* and similar leaves could be assigned to this genus. Bose & Manum (1991) have figured shoot fragments found in association with *Sciadopityoides nathorstii* (Halle) from the Lower Cretaceous of West Greenland. The leaf scars on these shoots are distinctly round, as are the abscission scars at the bases of *S. nathorstii* leaves (Bose & Manum 1990, fig. 3) but it is not clear from the drawings whether there are distinct sutures between leaf bases as in *Sulcatocladus*. However, Manum & Bose (1990) have figured other shoots associated with *Sciadopityoides*-like leaves in which the photographs (Bose & Manum 1990, pl. 2, figs 4, 5) clearly show sutures between decurrent leaf bases exactly as in *Sulcatocladus*. Such shoots, of undoubted coniferous affinity, being repeatedly found in association with leaves of the *Sciadopityoides/Pseudotorellia* type, suggests to us that we need to re-examine all leaves of this type assigned to the Ginkgoales, particularly *Pseudotorellia* species, with the question of associated shoots in mind.

? Family TAXACEAE
Genus *TORREYITES* Seward

1919   *Torreyites* Seward: 419. [formal diagnosis not given]
1920   *Torreyites* Seward; Seward & Sahni: 35.

TYPE SPECIES.   *Tumion carolinianum* Berry 1908: 383, figs 1–3.
   It should be noted that Seward misspelled Berry's specific epithet *carolinianum* as *carolinanum* (Seward 1919: 420) and this was repeated by Andrews (1970: 216).

DIAGNOSIS.   Needle-shaped or elliptical fossil leaves with haplocheilic stomata confined to two well-marked longitudinal grooves on lower surface; lacking prominent midrib on upper surface of lamina.

REMARKS.   The genus *Torreyites* was erected by Seward (1919) for Cretaceous and Tertiary fossil leaves referred to the modern genus *Torreya* Arnott but for which he found the evidence unconvincing. Seward did not formally diagnose the genus but applied it to the type species *Torreyites carolinianum* (Berry) Seward (1919: 420) and listed several others for which neither cuticles nor seeds were known. Since that time the genus has been little used and successive authors (Florin 1958; Krassilov 1967, 1973; Harris 1979; Bose & Manum 1990) have chosen to place fossil leaf species resembling *Torreya* within the living genus, usually on the basis of cuticle evidence alone. Given the lack of evidence from reproductive structures, we feel that *Torreyites* Seward remains a useful and more appropriate genus, in particular for the extremely fragmentary material dealt with in the present work. Its use does not imply the possession of *Torreya*-like ovules and the certainty of attribution to the Family Taxaceae. Some fossil species are indeed close in cuticular detail to modern *Torreya* and it is likely that they are closely related. However, with only cuticular evidence there always remains a doubt and it seems to us preferable to place them in a separate genus. We are therefore returning to the use of the form-genus *Torreyites* as proposed and used by Seward (Seward 1919; Seward & Sahni 1920).

Torreyites detriti sp. nov.   Figs 35–40

1976   12 Cycad BeC Oldham (Code used instead of Linnean binomial): 450; pl. 61, figs 5–9.
1976   31 Taxod ScA Oldham (Code used instead of Linnean binomial): 462; pl. 73, figs 1–6.

DIAGNOSIS.   Needle-shaped or elliptical leaf, 1–3 mm wide or more, up to at least 15 mm long, with mucronate apex and base without distinct petiole. Stomatal grooves on lower surface 70–210 µm wide, about 500 µm apart on either side of the midline; stomata scattered within groove.
   Ordinary epidermal cells of upper surface 4-sided or irregular in shape with more or less sinuous anticlinal walls, typically 30 (10–73) µm long and 26 (10–47) µm wide; cells in median region elongate, 47 (20–78) µm long and 17 (8–29) µm wide, arranged in longitudinal files. Outer surface often bearing thickened, longitudinal, cuticular ridges; two continuous ridges along each file of cells.
   Ordinary epidermal cells of non-groove regions of lower surface mostly 4-sided with straight or moderately sinuous anticlinal walls, arranged in longitudinal files. Outer surface often bearing thickened, longitudinal ridges similar to upper surface. Cells in median region typically 44 (21–71) µm long and 17 (8–29) µm wide; cells in marginal regions 36 (18–65) µm long and 19 (10–37) µm wide. Cell files at edges of stomatal grooves more strongly ridged, bearing both short round papillae and finger-like papillae up to 35 µm long or more; sometimes fused laterally to form cutinized fringe overhanging stomatal groove.

Stomata densely packed within groove, longitudinally or obliquely orientated, surrounded by sparsely scattered isodiametric ordinary epidermal cells up to 20 μm across. Stomatal apparatus comprising guard cells each about 35 μm long and 8 μm wide, with square-ended polar appendages, surrounded by a ring of about 10 subsidiary cells, each bearing a long, hollow papilla overhanging a slit-like stoma. Subsidiary cells of adjacent stomata often in contact but never shared.

NAME.   After Detritus, troll and member of the Ankh-Morpork City Watch in the Discworld novels of Terry Pratchett.

HOLOTYPE AND LOCALITY.   V.64608, Fig. 35E, a dispersed leaf fragment from the plant debris beds near Hanover Point, on the South West coast of the Isle of Wight. Wessex Formation; Barremian.

MATERIAL AND OCCURRENCE.   All specimens of *Torreyites detriti* sp. nov. figured here have been found as well-preserved dispersed leaves within the 'plant debris beds' of the Wessex Formation. Figs 35A–F, I–O; 36A–N; 37A–G; 38A–C; 39; 40 show material from the South West coast of the Isle of Wight; Fig. 35G, H shows material from Swanage, Dorset. *T. detriti* was also identified by Oldham (1976) in samples from Dorset at Worbarrow and Swanage, the South West coast of the Isle of Wight, and also from the Ashdown Beds at Hastings in Sussex. Stratigraphical range: Berriasian – Barremian.

DESCRIPTION AND DISCUSSION.   The leaf specimens of *Torreyites detriti* sp. nov. recognised so far are elliptical (Figs 35A; 36A, D, E, J, L) or needle-shaped (Figs 35B, C; 36B, C, H, I). Although most leaves can readily be identified either as needles or as wider elliptical forms, apparently intermediate forms can also be recognised (Fig. 36F, G). There is no distinct petiole and in some leaves the extreme base appears to be a round leaf-scar (Fig. 35D) which almost certainly indicates abscission. The basal region is commonly twisted (Figs 35D, F; 36J–N), a feature which has recently been discussed in some detail by Watson & Harrison (1998) in relation to the leaves of *Pseudotorellia linkii* using living *Abies* for comparison. If, as is quite likely, the leaves of *T. detriti* were borne in two distinct ranks then some degree of twisting would be related to leaf insertion in the living shoot. Conifer shoots of this type present the thickly cutinized adaxial surface of all the leaves uppermost but this is a secondary dorsiventrality superimposed on spiral leaf insertion. In order to achieve this, some leaves are twisted at the base more than others (Watson & Harrison 1998, fig. 1D). Such twisting can also be simulated in the laboratory by leaving pieces of shoot or isolated leaves exposed for a few days. The twisting of leaf bases in *Torreya nucifera* becomes much more exaggerated when left to dry. We cannot rule out the possibility, of course, that the twisting is related to post-mortem drying and shrinkage in *T. detriti*.

The leaf tip is frequently absent (Fig. 35E), perhaps indicating a scarious nature in life. Where present, the apex is mucronate (Fig. 35G, H). The frequent absence of the extreme tip in conifer leaves of this type is very common, has repeatedly been discussed in the literature and is mentioned here under the description of *Sciadopityoides* above.

The two longitudinal stomatal grooves on the lower surface of the leaf of *T. detriti* (Figs 35A–I; 36A–N) are usually filled with sediment and show as pale bands on the shiny black leaves. Thus they stand out as a very distinctive feature which makes the leaves of this species easy to spot and pick out of bulk debris material. After cleaning in hydrofluoric acid the stomatal grooves appear brown and dull and still stand out clearly (Fig. 35A, C) against the shiny, black, non-stomatal regions. Quite small cuticle scraps with just a portion of the distinctive groove are for this reason also easy to recognise.

The upper surface of the leaf is less remarkable (Fig. 35J) with the upper cuticle (Fig. 35J–O) showing the irregular shape of the ordinary epidermal cells of the marginal areas contrasting with the four-sided elongate cells arranged in longitudinal files over the midrib (Fig. 35K, L). The outer surface of the upper cuticle bears rather distinctive longitudinal ridges (Fig. 35M, N) and the light microscope shows that there are generally two of these ridges per longitudinal file of cells (Fig. 35O).

The lower cuticle (Figs 37A–G; 38A–C; 39; 40) shows the longitudinal files of four-sided ordinary epidermal cells outside the grooves; those in the median regions more elongate than those of the marginal regions (Fig. 37A, B). The outer surface often bears the same longitudinal ridges seen on the upper cuticle being more pronounced in the few files of cells nearest to the groove (Figs 37C; 38A, B). These cell files also bear short, round papillae, usually with depressed tips (Fig. 38A, B) and longer, hair-like papillae which overhang the groove individually, or fuse laterally to form long cutinized fringes (Figs 37C, D; 38A, B).

There is a high density of longitudinally or obliquely orientated stomata scattered within the grooves (Figs 37A; 39; 40), but there are also many long papillae on the subsidiary cells and the groove margins obscuring the details of the stomata, particularly an outside view in the SEM (Figs 37C; 38A, E). In the light microscope they are also difficult to discern (Fig. 37E) but see Fig. 41 and comments below. The inner surface of the groove in the SEM shows the stomatal apparatus to consist of a pair of guard cells with square-ended polar appendages (Fig. 37F, G), and slit-like openings (Figs 39; 40), surrounded by a ring of up to 10 or so subsidiary cells (Fig. 37F, G). Subsidiary cells of adjacent stomata are often in contact but never shared (Figs 37A; 39).

Oldham (1976) described two types of cuticle fragments, 12 Cycad BeC which he described as cycadalean and 31 Taxod ScA as a *Sciadopitys*-like leaf. However, additional material from Oldham's and other localities has shown them to be identical to *T. detriti*. Fig 41 shows drawings of a leaf from the Lower Cretaceous of Poland made by Watson during a visit by the late Dr Maria Reymanówna to the late Professor T.M. Harris in 1962. Reymanówna (pers comm. 1962) intended to describe this leaf as *Torreya* or *Torreyites* but we have no knowledge of her having done so. From the drawings it appears to us to be identical to *Torreyites detriti* but the present whereabouts of the leaf are unknown. However, it is likely that further specimens could

Fig. 35 A–O   *Torreyites detriti* sp. nov. All from Wessex Formation. **A–I, L–O,** from the South West coast of the Isle of Wight; **J, K** from Swanage, Dorset. **A,** elliptical leaves, L–R: V.64595–V.64599, × 2.5; **B,** needle-shaped leaves, V.64600–V.64606, × 2.5; **C,** single long needle, V.64607, × 5; **D,** leaf fragment showing round leaf-scar at base and basal twisting, V.64606, × 5; **E, holotype,** leaf dissected to show both upper and lower cuticle, V.64608, × 10; **F,** leaf fragment showing twisted base and longitudinal grooves, V.64609, LM, × 10; **G,** leaf fragment with mucronate apex, V.64610, LM, × 25; **H,** leaf tip mounted on stub lower surface uppermost, showing longitudinal grooves, V.64611, SEM, × 25; **I,** lower cuticle showing longitudinal grooves, V.64612, LM, × 25; **J,** upper cuticle showing cell elongation over midrib, V.64612, LM, × 25; **K,** upper cuticle showing more regular, elongate ordinary epidermal cells in longitudinal rows over midrib towards right, and less regular cells of marginal regions to left, V.64612, LM, × 125; **L,** inside view of upper cuticle showing more regular, elongate ordinary epidermal cells in longitudinal rows over midrib towards right, and less regular cells of marginal regions to left, V.64613, SEM, × 125; **M,** outer surface of upper cuticle bearing regular longitudinal ridges, V.64614, SEM, × 125; **N,** longitudinal ridges in detail, V.64614, SEM, × 500; **O,** light micrograph of upper cuticle focussed to show relationship between cells and ridges, V.64612, LM, × 500.
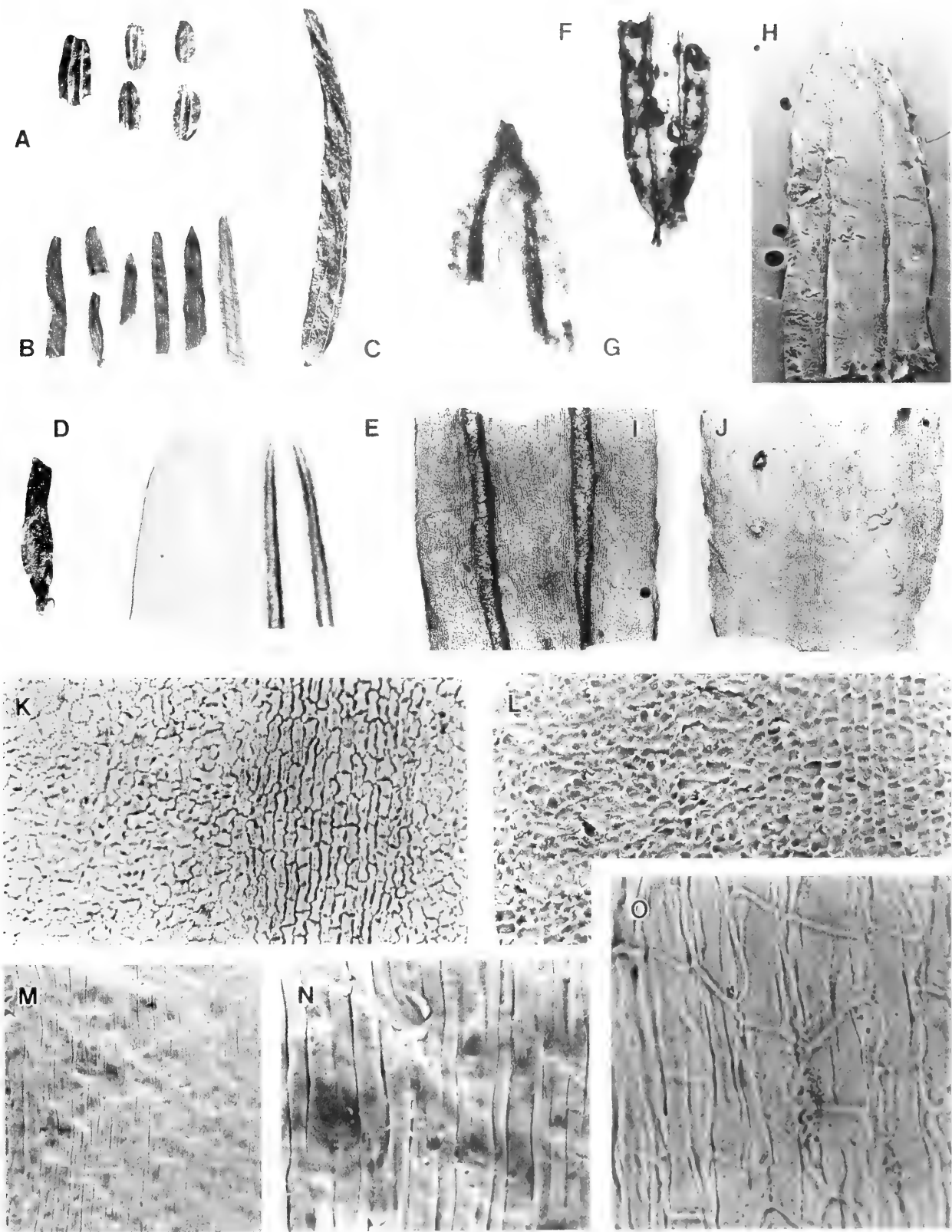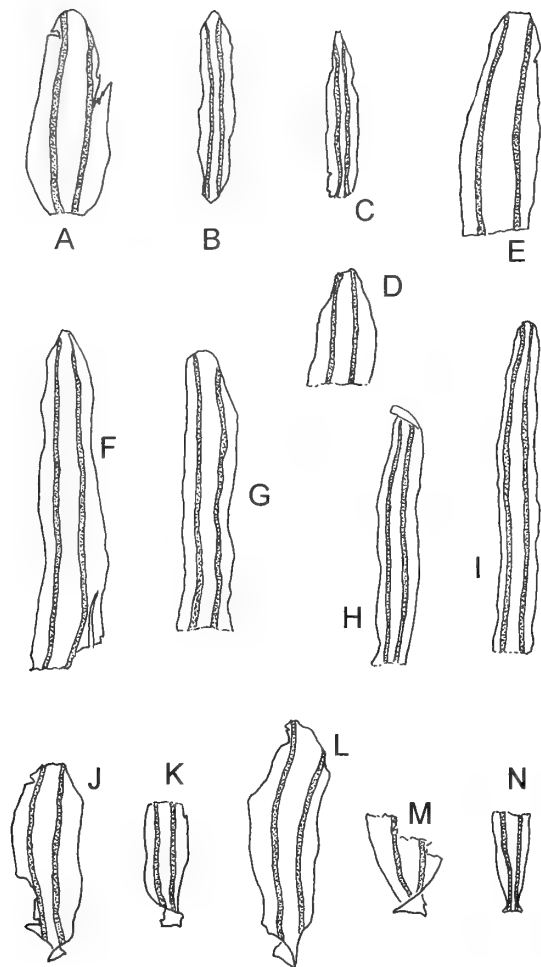
Fig. 36 A–N *Torreyites detriti* sp. nov. All dispersed leaves from Wessex Formation, Isle of Wight showing variety of shape and positions of stomatal grooves. **A–N,** V.64615–64628, all × 5; **A–I,** leaves with apex more or less intact; **J–N,** leaves with twisted bases.

be obtained by bulk maceration of debris material from the Lower Cretaceous beds near where the original is probably from.

It is possible that the small elliptical leaves represent juvenile leaves, but leaf heteromorphism is not seen in modern *Torreya* and there is far too little evidence to draw any conclusion about whether this is the case in *T. detriti*.

COMPARISON.   *Torreyites detriti* is the only species of this genus to be recognised within the English Wealden. Fig. 38A, B shows the resemblance of *T. detriti* to the living species *Torreya californica* Torrey which also has highly papillate stomatal grooves (Fig. 38C). The leaves of *T. californica* are, however, often four times the size of the largest leaf of *Torreyites detriti* discovered so far.

All the species resembling *T. detriti* are referred to the genus *Torreya*, none of them on the basis of anything other than gross morphology and cuticle of leaves. Three of these are known from the Lower Cretaceous. *Torreya arctica* Bose & Manum (1990) from Spitsbergen is of a similar size to *T. detriti* but has stomata with fewer subsidiary cells confined to stomatal bands which are not sunken and which lack highly papillate margins. *Torreya bureica* Krassilov (1973) from the Bureja Basin is of a similar size and shape to the

elliptical specimens of *T. detriti* and bears longitudinal ridges along the leaf surface. The ordinary epidermal cells are, however, much more elongate than those of *T. detriti*. *Torreya nicanica* Krassilov (1967) from South Primorya differs considerably in having a short petiole and stomata which are arranged in rows.

Several other Mesozoic species with *Torreya*-like leaves have been described. *Torreya gracilis* Florin emend. Harris (1979) from the Middle Jurassic of Yorkshire is of a similar size to *T. detriti*, but differs in having a short flat petiole, a flat leaf surface, much more elongate ordinary epidermal cells and a midrib marked by broader, rather than narrower, cells on the upper cuticle. *Torreya valida* Florin (1958) from the Middle Jurassic of Yorkshire has more elongate ordinary epidermal cells and much broader stomatal grooves than those of *T. detriti*. *Torreya moelleri* Florin (1958), from the Middle Jurassic of Bornholm, Denmark, has a much longer leaf and the stomata, which have fewer subsidiary cells, are arranged in rows. *Torreya longifolia* Gomolitzky (1964) from the Jurassic of central Asia has larger leaves with more elongate ordinary epidermal cells and stomata with fewer subsidiary cells. *Torreyites carolinianus* (Berry) Seward (1919), from the Middle Cretaceous of North Carolina, is of a similar size to *T. detriti* but the description by Berry (1908) shows that the leaves taper much more gradually towards the apex and that the stomata tend towards transverse rather than longitudinal orientation.

PALAEOECOLOGY

The species described here, with the exception of *P. linkii*, have been found exclusively within debris beds and in a more or less fragmentary state, suggesting that they may have been transported a fair distance from their natural habitat, presumably on higher ground. The addition of the species described here to the Wealden floral list indicates that upland ecology, particularly that of areas draining into the Wessex Basin, may have been more complex than previously understood. Whilst dense forests of the cheirolepidiaceous conifer *Pseudofrenelopsis parceramosa* undoubtedly dominated large areas of higher ground (Watson & Alvin 1996: 23), there is growing evidence of mixed communities of ginkgoes, czekanowskialeans and needle-leaved conifers.

The wild origins and ecology of *Ginkgo biloba*, the single extant member of the Ginkgoales, are poorly known. It has been widely cultivated in China and Japan for centuries and is known to be native to Eastern China, where it might still occur as small populations in mixed conifer-broadleaf forests in remote mountain valleys (Page 1990a). *Ginkgo* prevailed in moist and moderately warm conditions during the Cenozoic (Uemura 1997), and its tendency for mesic habitats may well have evolved earlier. Vakhrameev (1991) certainly regarded the Ginkgoales as a mesophilic group, attributing their sharp reduction in the European province of the Late Jurassic to increased aridity.

Little is known about the ecology of the Czekanowskiales but a wet and warm climate is thought to have been favourable for *Czekanowskia* (Samylina & Kiritchkova 1993: 282), and both *Czekanowskia* and *Phoenicopsis* are important within the humid, moderately warm and seasonal conditions of the Early Cretaceous Siberian-Canadian region (Vakhrameev 1991). The apparent disappearance of the Czekanowskiales from the Euro-Sinian region was noted by Vakhrameev (1991: 127) as one of the most striking differences between the two regions during the Early Cretaceous. However, the discovery of *Czekanowskia anguae* and *Phoenicopsis rincewindii* in the English Wealden provides evidence which suggests
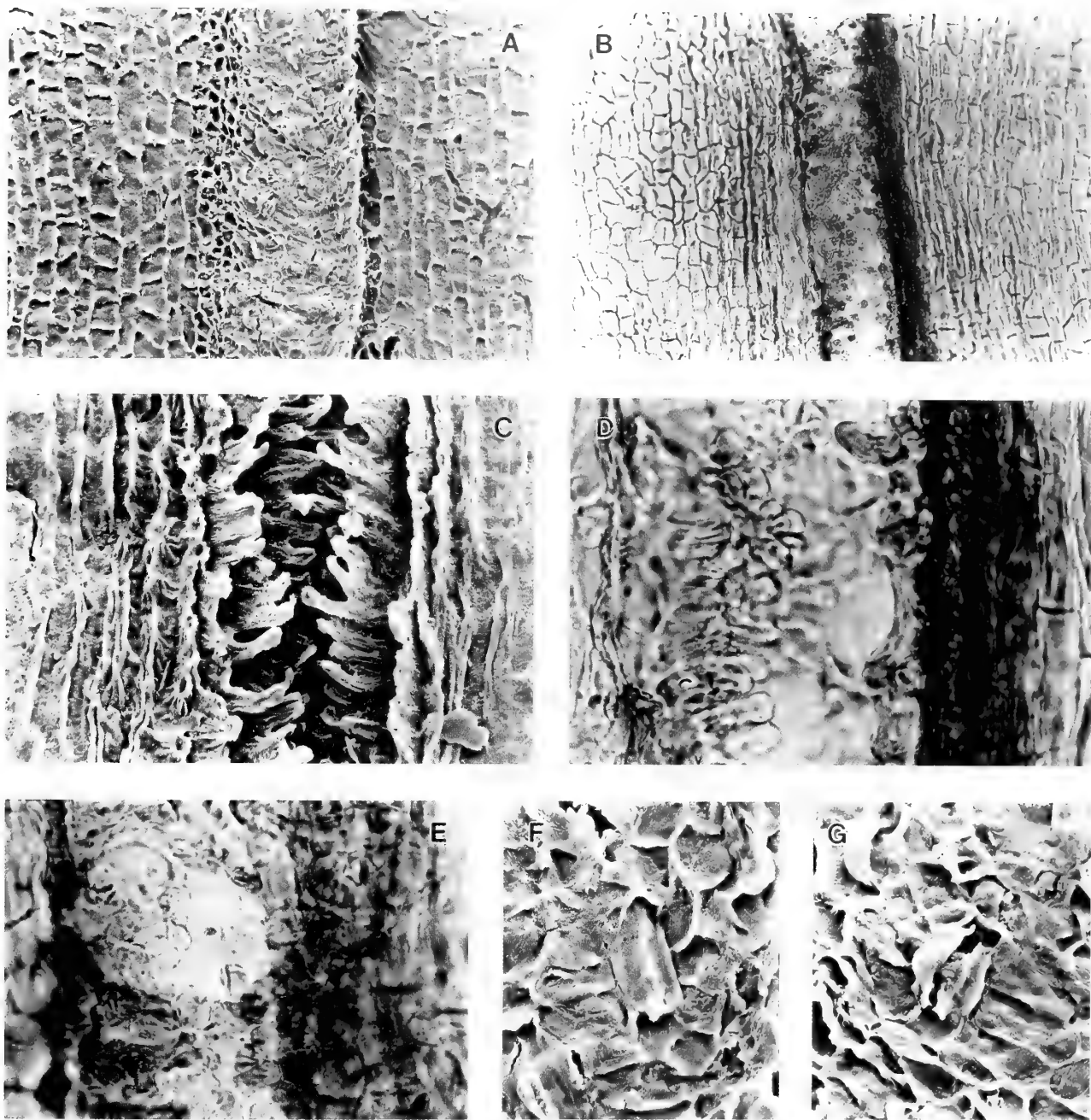
Fig. 37 A–G *Torreyites detriti* sp. nov. All lower cuticle. **A,** inside of lower cuticle showing longitudinal groove, with median region to right and marginal region to left, V.64613, SEM, × 125; **B,** lower cuticle showing longitudinal groove, with median region to right and marginal region to left, V.64612, LM, × 125; **C,** outer surface showing ridges, small round papillae with depressed tips and long papillae overhanging groove, V.64629, SEM, × 500; **D,** groove with long marginal papillae forming overhanging fringe (left-hand margin) or obscuring groove individually (right-hand margin), V.64612, LM, × 500; **E,** single stoma obscured by papillae, V.64612, LM, × 500; **F,** inside of single stoma, showing ring of subsidiary cells surrounding pair of guard cells, V.64613, SEM, × 500; **G,** inside of single stoma, showing guard cells with square-ended polar appendages, V.64613, SEM, × 500.

that these regions shared more common features than has previously been supposed. This is supported by the new occurrence in the English Wealden of types of needle-leaved conifers commonly found in other Cretaceous floras (Vakhrameev 1991). Members of the Taxaceae are slow growing and long-lived, typically occurring within sheltered forest vegetation, often in small local populations in damp, valley-bottom sites not subject to severe summer desiccation (Page 1990b). If *Torreyites detriti* does belong to this family, it would be reasonable to conclude that it occupied a similar niche.

Modern *Ginkgo* is deciduous, and Zhao *et al* (1993) have described *G. manchurica*, from the younger Mesozoic of North East China, occurring in thick masses of detached leaves which clearly indicate
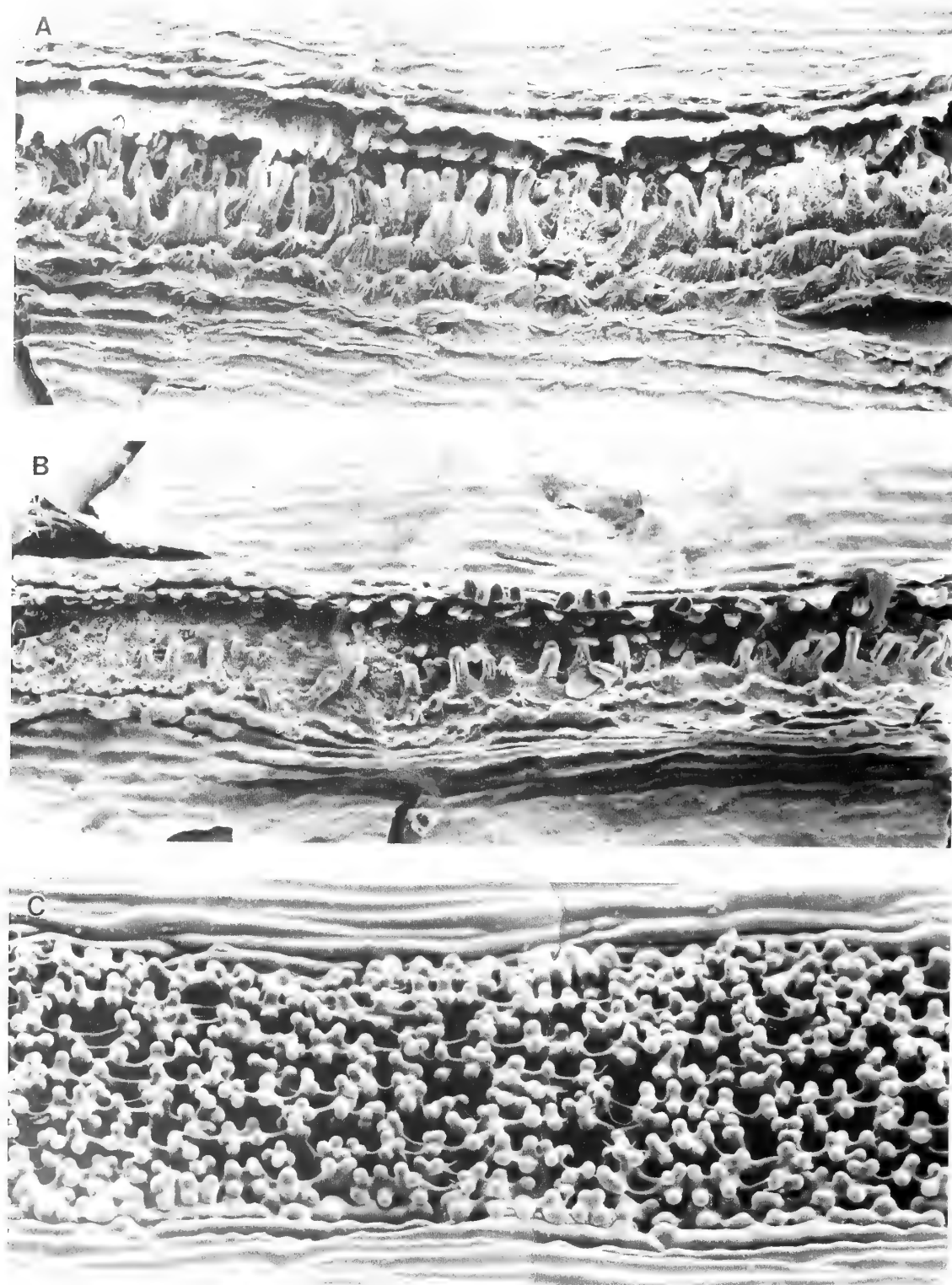
Fig. 38 A, B *Torreyites detritii* sp. nov. Wessex Formation, Isle of Wight, showing stomatal groove on lower cuticle, SEM, × 200. **A,** highly papillate groove, V.64630; B, less papillate groove, V.64629.

Fig. 38 C *Torreya californica* Torrey. Stomatal groove on lower cuticle, SEM, × 200.
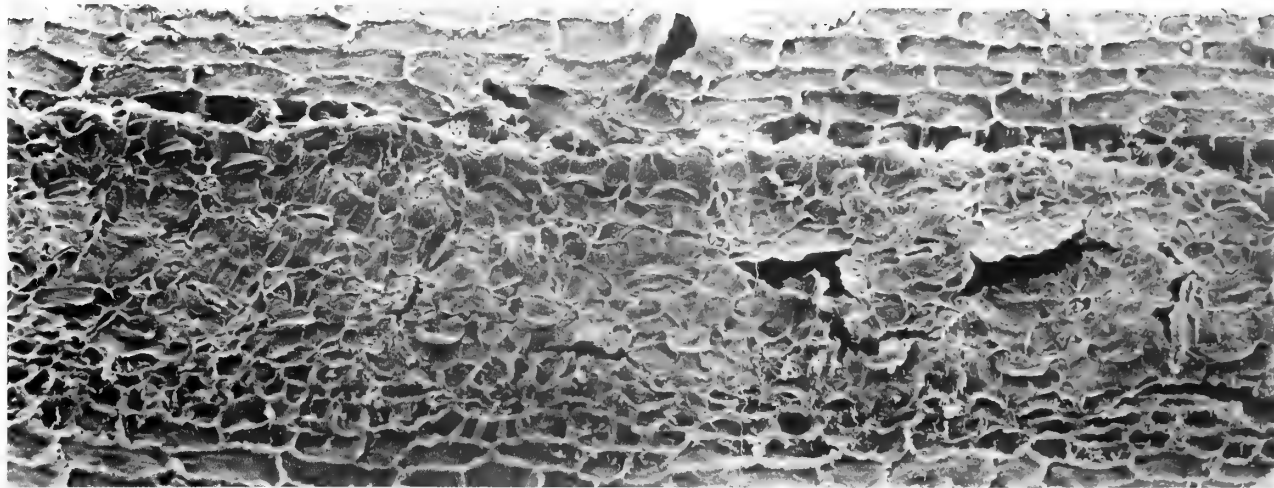
Fig. 39 *Torreyites detriti* sp. nov. From Wessex Formation, Isle of Wight. Inside of lower cuticle showing stomata scattered within longitudinal groove, SEM, V.64613, × 200.
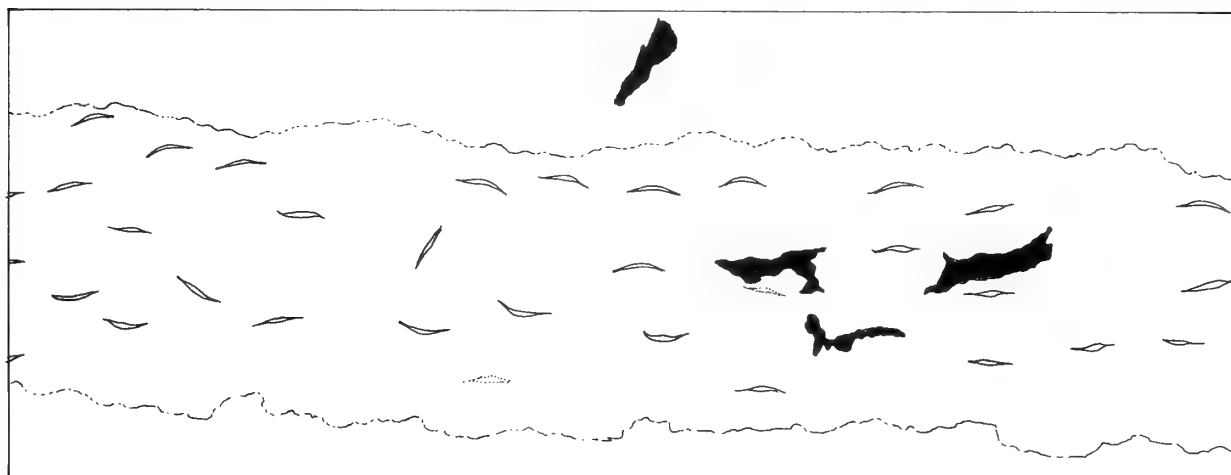
Fig. 40 *Torreyites detriti* sp. nov. From Wessex Formation, Isle of Wight. One stomatal groove showing distribution of stomata and orientation of slit-like stomatal openings, V.64613, × 200.

that this species was also deciduous. Examples of fossil populations representing mass leaf drops (brachyblasts) have been noted as a widespread phenomenon in *Phoenicopsis*, *Czekanowskia* and *Sphenobaiera* by Vakhrameev (1991). *Pseudotorellia linkii* occurs in a similar type of deposit in Dunker's '*Abietites* leaf coal' in the Wealden of Germany, though such concentrations have not been recognized in the English Wealden. Bose & Manum (1990, 1991) have also described needle-leaved conifers of the *Pseudotorellia/ Sciadopityoides*-type in pure leaf coals together with *Sulcatocladus*-type shoots (see discussion above). Clearly, all these occurrences of ginkgoalean, czekanowskialean and coniferalean brachyblasts indicate deciduousness, which itself indicates seasonality of some kind.

This scenario of mixed gymnosperm forests in moister valleys is not inconsistent with the current consensus view of the climate of the Wealden, as drawn from a wide range of disciplines by Allen (1998). He describes a very warm, seasonal 'Mediterranean' climate with occasional equable humid periods and generally wetter conditions on the upland massifs than in the plains. However, the presence of the species described here suggests that localized upland areas may have

remained moist for sustained periods, allowing the development of mixed forest groves. It is hoped that further studies of plant debris material will continue to improve our understanding of Wealden palaeoecology and climate.

Fig. 41 A–C *Torreyites* leaf from Lower Cretaceous of Poland. **A,** single elliptical leaf showing two stomatal grooves, × 7.5; **B,** close up of one stomatal groove showing long hair-like papillae densely covering stomata in pit, × 30; **C,** single stomatal opening ringed by hollow, finger-like hairs, × 500.

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APPENDIX

Details of specimens figured in this paper.

Czekanowskia anguae sp. nov.
  Worbarrow Bay, Dorset:
    V.64520, **holotype**. Figs 1A, B.
    V.64521, Figs 1C, D, G; 3B, E.
    V.64523, Figs 1F; 2A, B.
    V.64524, Fig. 1I.
    V.64525, Fig. 1J.
  Mupe Bay, Dorset:
    V.64522, Figs 1E, H; 3A, C, D, F.

Phoenicopsis rincewindii sp. nov.
  Hastings, East Sussex:
    V.64526, Figs 4A, C, F; 5A -C; 6A, C.
    V.64527, **holotype**, Figs 4B, D, E, G–J; 6B, D, E.

Ginkgoites weatherwaxiae sp. nov.
  Worbarrow Bay, Dorset:
    V.64528, Fig. 7A.
    V.64529, Figs 7B, F.
    V.64530, **holotype**, Figs 7C; 8B.
    V.64531, Figs 7D; 8F.
    V.64532, Figs 7E; 11F.
    V.64533, Figs 7G, H.
    V.64534, Fig. 8A.
    V.64535, Fig. 8C..
    V.64536, Fig. 8D.
    V.64537, Fig. 8E.
    V.64538, Fig. 8G.
    V.64539, Figs 8H; 11A, E .
    V.64540, Figs 9A–F.
    V.64541, Figs 10A, E.
    V.64542, Figs 10B–D, F; 11B–D, G, H.

Ginkgoites nannyoggiae sp. nov.
  Worbarrow Bay, Dorset:
    V.64543, Fig. 12A.
    V.64544, Fig. 12B.
    V.64547, Figs 12G; 15A, E.
  Galley Hill, East Sussex:
    V.64545, **holotype**, Figs 12C; 13A–C; 14A–C; 15C, F
  Mupe Bay, Dorset:
    V.64546, Figs 12D–F; 14D; 15B, D.

Ginkgoites garlickianus sp. nov.
  South-west coast, Isle of Wight:
    V.64548, **holotype**, Figs 16A C, E; 17A, B; 18A, C; 19B, C, E, F.
    V.64549, Figs 16D, F, G; 18B.
    V.64550, Fig. 19A.
    V.64551, Fig. 19D.

Ovule attributed to Ginkgoites weatherwaxiae
  Worbarrow Bay, Dorset:
    V.64552, Figs 20A G; 21

Pseudotorellia linkii (Römer)

Angiarsuit, West Greenland:
    V.19021b, Figs 22C, F (figd. Seward 1926: text-fig.16Aii; Watson & Harrison 1998: fig. 4C, D; formerly holotype of *Pityophyllum crassum* Seward).
Fairlight, near Hastings, East Sussex:
    V.51525, Fig. 23A (figd. Watson 1969: fig. 61; Watson & Harrison 1998: figs 7C, D, 11C; formerly holotype of *Pseudotorellia heterophylla* Watson).
    V.51527, Fig. 23D (figd. Watson 1969: fig. 60; Watson & Harrison 1998: fig. 11D).
    V.51528, Fig. 23B (figd. Watson 1969: fig. 62; Watson & Harrison 1998: fig. 11B).
    V.64289, Figs 22J, M N, (figd. Watson & Harrison 1998: figs 12C, D, F; 13C, E).
Haddocks Rough, near Hastings, East Sussex:
    V.64239, Fig. 23E (figd. Watson & Harrison 1998: fig. 9A); collected by T. C. B. Oldham.
Galley Hill, East Sussex:
    V.64240, Fig. 23F (figd. Watson & Harrison 1998: fig. 9B); collected by T. C. B. Oldham.
    V.64243, Fig. 23C (figd. Watson & Harrison 1998: fig. 11E – but note wrong locality); collected by T. C. B. Oldham.
    V.64290, Fig. 22K (figd. Watson & Harrison 1998: fig. 13D); collected by T. C. B. Oldham.
    V.64553, Fig. 22G .
Worbarrow Bay, Dorset:
    V.64196 – 64200, Figs 22B, left to right (figd. Watson & Harrison 1998: fig. 3D).
    V.64202, Fig. 22E (figd. Watson & Harrison 1998: fig. 7B).
Düingen, Germany:
    V.64174 – 64195 (previously V.862), Figs 22A, left to right (figd. Watson & Harrison 1998: fig. 1A).
    V.64203 (previously V.862), Figs 22H, I (figd. Watson & Harrison 1998: figs 8B, D).
    V.64205 (previously V.862), Fig. 22L (figd. Watson & Harrison 1998: fig. 8E).
    V.64249 (previously V.19763), Figs 22D (figd. Watson & Harrison 1998: figs 3B; 5A, B).
    V.64250 (previously V.19763), Fig. 23G (figd. Watson & Harrison 1998: figs 5M; 9D, E; 15A, 23G); now on microscope slide.

Pseudotorellia vimesiana sp. nov.
  Hastings, East Sussex:
    V.20434, Figs 25A, B.
    V.64554, Fig.24A.
    V.64556, Figs 24C–L; 25E, F.
    V.64557, Fig. 25C.
    V.64558, Fig. 25D.
  Mupe Bay, Dorset:
    V.64555, Fig. 24B, **holotype**.

Sciadopityoides greeboana sp. nov.
  Galley Hill, East Sussex:
    V.64559 – 64567, Fig. 26A left to right (V.64560 also shown in Fig. 26F); V.64560 is the **holotype.**
    V.64568, Fig. 26B.
    V.64569, Fig. 26C.
    V.64570, Fig. 26D.
    V.64571, Fig. 26E.
    V.64572 – 64585, Figs 27A–N.
    V.64586, Fig. 27O.
    V.64587, Figs 28A,F; 29A, B, E, F; 30A, B.
    V.64588, Figs 28B–E; 29C, D, G, H.

Sulcatocladus robustus Watson & Harrison
  Galley Hill, East Sussex:
    V.64291, Fig. 31G (figd. Watson & Harrison 1998: fig. 17H); collected by T. C. B. Oldham.
    V.64590, Fig. 31D.
  Worbarrow Bay, Dorset:
    V.64589, Fig. 31B, C..
  Düingen, Germany:
    V.64207 (formerly V.862), Fig. 31E, F, **holotype**, (figd. Watson & Harrison 1998: fig. 17E, G).
    V.64256 (formerly V.19763), Fig. 31Ai (figd Watson & Harrison 1998: fig. 17A; 19C, D).
    V.64257 (formerly V.19763), Fig. 31ii (figd. Watson & Harrison 1998: fig. 17B).
    V.64292 (formerly V.862), Fig. 31H (figd Watson & Harrison 1998: fig. 17F, I).

Sulcatocladus dibbleri sp. nov.
  Hastings, East Sussex:
    V.64591, Figs 34A, C.
    V.64592, Fig. 34B.
  Galley Hill, East Sussex:
    V.64593, Figs 34D–G, **holotype.**
    V.64594, Fig. 34H.

Torreyites detriti sp. nov.
  South west coast, Isle of Wight:
    V.64595 – 64599, Fig. 35A.
    V.64600 – 64606, Fig. 35B (V.64606 also shown in Fig. 35D).
    V.64607, Fig. 35C.
    V.64608, Fig. 35E, **holotype.**
    V.64609, Fig. 35F.
    V.64612, Figs 35I–K, O; 37B, D. E.
    V.64613, Figs 35L; 37 A, F, G; 39; 40.
    V.64614, Figs 35M, N.
    V.64615–28, Figs 36A–N respectively.
    V.64629, Figs 37C, 38B.
    V.64630, Fig. 38A.
  Swanage, Dorset:
    V.64610, Fig. 35G.
    V.64611, Fig. 35H.

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